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E. RAY LANKESTER.

It is now five-and-twenty years since Professor Lankester first undertook the task of editing the 'Quarterly Journal of Microscopical Science,' and by issuing the present number his colleagues desire to mark the occasion, and at the same time to take the opportunity of offering to him their hearty congratulations on the success which has attended this quarter of a century of effort on his part.

The Journal was founded in the year 1853 by the publisher, Mr. S. Highley, and was edited by Dr. Edwin Lankester and Mr. George Busk. In 1856 the publisher's business was transferred to Mr. John Churchill, with which firm it has remained ever since. Up to 1868 the Journal published the 'Transactions of the Royal Microscopical Society of London,' but in 1869 the Society started its own publication, and a new editorial arrangement of the Journal was made. Mr. George Busk retired, and Mr. Ray Lankester, who had lately taken his degree at Oxford, joined his father in the editorship.

Mr. Ray Lankester's connection with the Journal began in 1863 with the publication of a paper "On our Present Knowledge of the Gregarinæ," followed in 1864–5 by a memoir, in three parts, on "The Anatomy of the Earthworm." In 1865 he suggested the publication of a Quarterly Chronicle of the progress of Histology and Microscopic Investigation, and joined Mr. Busk in its preparation. Curiously enough, this feature has been abandoned since 1872, whilst the Royal Microscopical Society has taken the task in hand, and produces an admirable and extensive record.

In 1872 Ray Lankester's father ceased to take part in

editing the Journal, and was succeeded by Dr. J. Frank Payne. Lankester and Payne added Mr. Thiselton Dyer (now Director of Kew Gardens) to their editorial body in 1873, and he was succeeded in 1876 by Mr. Archer, of Dublin, the Secretary of the Dublin Microscopical Club, and the author of so many interesting discoveries among fresh-water Rhizopoda. In 1877 Dr. Payne retired, and Dr. Klein joined the editorial staff.

In 1878 a further change was made. Professor Lankester became sole editor, with the co-operation of Archer, Francis Balfour, and E. Klein. This arrangement has continued ever since, with various changes in the list of those co-operating. Thiselton Dyer returned for a few years as one of those giving his co-operation; and Moseley and Milnes Marshall have in turn assisted in the conduct of the Journal, and have published in it many of their most important papers, inducing their pupils to adopt the same mode of publication.

The number of contributions which this energetic policy attracted to the Journal soon made it necessary to enlarge it; and the term of Lankester's editorship has been marked by a continuous increase in the amount of letterpress and in the number and excellence of the plates. This has of necessity been accompanied by a rise in price. The original price was four shillings per number—the numbers being issued quarterly. At that time the volume consisted of some eight-and-twenty demy octavo sheets and twenty plates, mostly also octavo. The last volume contained thirty-six royal octavo sheets and forty-two plates, many of which were coloured, while the majority were of quarto size. The change from demy to royal octavo was effected at the commencement of 1883, and in 1890 the strict quarterly publication of the Journal was abandoned, so that more than four numbers could be issued in the year. During the eleven years which have elapsed since 1883 sixty-one numbers, divided into fifteen volumes, have been issued; so that the increase in size and price has not only affected the magnitude of each number, but has been accompanied by an increased rapidity of publication.

Every reader will remember that Professor Lankester's energy has by no means been exhausted in merely editing the Journal, for besides his many writings elsewhere, he has published more than sixty memoirs in the pages of this Journal alone; and we may, perhaps, be permitted to mention a few of the more prominent of these—such as that on "The Development of the Pond Snail" (1874), which marks the starting-point of his well-known investigation of the development of Mollusca; the "Notes on the Embryology and Classification of the Animal Kingdom" (1877), which exercised so great an influence upon the whole tendency of morphological speculation; the descriptions of Limnocodium (1880); the series of memoirs on Apus and Limulus (1881—1884), and on Rhabdopleura (1884); the first description of the atrio-cœlomic funnels in Amphioxus (1875), and the subsequent memoir on the anatomy of the same animal, together with the account, commenced in conjunction with his pupil Mr. Willey, and continued by Mr. Willey alone, of the later history of its remarkable larva.

It would be useless to enumerate all the naturalists who have contributed to the Journal since Professor Lankester's successful enterprise has made it the chief medium of publication for English morphological work; but it is interesting to notice that the contributors have constantly included foreign naturalists of distinction, including E. van Beneden, Bowditch, Carrière, Claparède, Dollo, Giard, Hubrecht, Iijima, Ischikawa, Kingsley, Mitsukuri, H. F. Osborn, Oudemans, Packard, Patten, Pelseneer, Pouchet, Ranvier, Whitman, and others. Some of these have taken the opportunity, by contributing to the present number, of joining in the hearty congratulation on his past achievement, and sincere good wishes for the future, which Professor Lankester's associates now offer to their chief.

A. SEDGWICK.

April, 1894. W. F. R. WELDON.

A Contribution to the Morphology of Bacteria.

By

E. Klein, M.D., F.R.S.,
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Hospital Medical School.

With Plate 1.

SINCE the classical papers on Bacteria published by Professor F. Cohn in the 'Zeitschrift der Biologie d. Pflanzen,' vols. i to iii, all bacteriologists have accepted the subdivision of the Schizomycetes into cocci, bacilli, and vibrios or spirilla, as representing the main morphological fundamental types. But by Lankester[1] and Zopfs' researches on Cladothrix dichotoma, and by Hauser's well-known and exhaustive work on 'Putrefactive Bacteria' ('Ueber Fäulnissbacterien,' Leipzig, 1885), it has become recognised that the shape under which a particular bacterial species presents itself depends both on the medium in which it grows, as also on certain inherent characters of the organism itself. Thus it has become recognised that while the elements of one species appear as often in the form of oval as of cylindrical cells, those of another retain, under almost all conditions, pre-eminently that of cylindrical cells. To name a few instances: (*a*) the Proteus vulgaris of Hauser. This organism—the organism of putrefaction par excellence—is known to occur in the most varied shapes, as cocci, oval forms, cylindrical and vibrionic forms; but when growing in gelatine plates at 20° C. it will be found that in the

[1] 'Quart. Journ. Micr. Sci.,' vol. xiii, 1873; vol. xvi, 1876.

first twenty-four to forty-eight hours the colonies are made up entirely of cylindrical bacilli, some of extreme length and forming very characteristic threads. The "swarming" out and the development of strands from such a colony are uniformly due to, and consist of, thread-like bacilli (see my article in Stevenson and Murphy's 'Treatise on Hygiene,' II, pl. ii); but later on, say after three or four days, when liquefaction of the gelatine has become extensive, the forms one meets are those various kinds described by Hauser as coccus forms, ovals, cylindrical cells, and vibrionic forms.

(*b*) The Bacillus filamentosus (which I found in sewage, and which I described in my article in Stevenson and Murphy's 'Treatise on Hygiene,' II, fig. 14) is, under all conditions of culture (gelatine, agar, broth, serum, &c.), always made up of cylindrical cells, either singly or in pairs, or forming longer and shorter chains.

The same applies to the Bacillus subtilis, the bacillus of swine erysipelas, and the bacillus of human typhoid fever.

(*c*) The Bacillus prodigiosus, on the other hand, remains under artificial cultivation in the various media pre-eminently of the spherical or slightly oval shape, while there are always present a few cylindrical forms, and it is owing to the greatly prevalent number of coccus forms that in former years this organism was described (Cohn, Schrötter) as the Micrococcus prodigiosus.

Another interesting point connected with the unstable shape under which some species appear is that while some, growing in one medium, appear under one particular shape, this changes when growing in a different medium. A group of bacteria are known, the essential biological character of which is that most of them produce acute septicæmic infection in one or the other rodent. To this group belong the bacillus of fowl cholera, of fowl enteritis, of Frettchenseuche, of Wildseuche, of swine fever, of the Middlesborough pneumonia, of grouse disease, the Bacillus coli, and others.

Now all these in their cultural characters in the different media have many points in common, as also the close resem-

blance of the acute disease they are capable of producing in rodents. But it is noticeable amongst them that while some preserve the same definite shape when grown in one species of animals or one kind of medium, this becomes changed under other conditions. Take, for instance, the bacillus of grouse disease: in the grouse itself, taken from the liver or cultivated in gelatine, it appears in a short oval form; but in the guinea-pig or in the mouse the cells are more commonly of a cylindrical form, and so also in the gelatine culture from the blood of these animals.

Amongst the best known examples of permanency of shape is that of the Bacillus anthracis; so much so that its cylindrical elements, single and in short and long chains in the blood of an animal dead of anthrax, have become as much the classical illustrations of typical bacilli as those of the Bacillus subtilis.

A. In the year 1883 (see this Journal, vol. xxiii) I have described a peculiar change of the anthrax bacilli in culture, in the course of which the typical cylindrical cells constituting the well-known threads become transformed into oval and spherical corpuscles, some containing vacuoles. This change was named a torula form, because some of the threads resemble in a remarkable manner the chains of cylindrical, oval, and spherical cells which are observed on Saccharomyces mycoderma of thrush. The direct connection between the typical cylindrical cells and the spherical and oval corpuscles (three and more times the diameter), and the division of these into similar corpuscles, was traced in many filaments through all intermediate stages (fig. 1).

At that time I insisted on these changes not being due to involution and degeneration, but belonging to an active phase of growth in the artificial media. In the first place it was then shown that this morphological change is observed already in an early stage of growth, when of degeneration there can be no question; besides, in later phases, after two, three, and more days' growth, the progress of the growth and the resulting filaments are again of the characteristic appearances. I have

within recent years almost constantly observed a similar change in early phases of the growth of anthrax bacilli in gelatine plates (beef bouillon; gelatine 10 per cent.; peptone 1 per cent.; salt 1 per cent.). Already in very early phases, when the colonies are only just visible as angular greyish spots, and when by their numerous outgrowing filamentous prolongations they become more and more connected with one another—that is, between twenty-four to forty-eight or seventy-two hours' incubation at 20° C.—numbers of these filamentous sproutings, examined in impression cover-glass specimens, are seen to be made up entirely or partially, not of the typical filaments composed of the cylindrical typical bacilli, but of large spindle-shaped spherical or oval elements, the protoplasm of which showing abundant vacuolation. In figs. 2 and 3 such growing outrunners of young colonies are accurately represented by photograms. There can be no question, then, of these forms being indicative of active growth; as a matter of fact, later on—that is after four days and more, as growth proceeds and liquefaction becomes pronounced—such forms do not obtain any more; the threads are all uniformly made up of the typical cylindrical bacilli.

When comparing the colonies of the thrush fungus, Saccharomyces mycoderma, or Oidium albicans, growing on gelatine plates, it will be found that the impression preparations obtained therefrom show in many filaments the very identical appearances; and that while some threads or parts of threads are composed of cylindrical cells, others are made up of oval, spindle-shaped, and spherical cells; the same local accumulation of the growing protoplasm as huge spindles or spheres, and the same vacuolation of the protoplasm are observed in both. I conclude from this that, although the Bacillus anthracis is a typical bacillus in the blood of animals infected with, or dead from, anthrax, and also in most conditions of artificial cultivation, it nevertheless under certain conditions (early stages of growing colonies on gelatine) assumes a character by which it closely resembles a Saccharomyces mycoderma, or perhaps Oidium, and thereby

probably it returns to an atavistic stage in its evolutional history.

B. The second microbe, by which a similar marked change is exhibited, is the Bacillus diphtheriæ. Löffler ('Mitth. aus d. k. Ges.,' vol. ii) first drew attention to the fact that the diphtheria bacillus, discovered by Klebs, shows on cultivation a curious segregation of its protoplasm, and a knob-like or club-shaped enlargement of one or both ends. Löffler, and after him others (Flügge, 'Mikroorganismen;' Baumgarten, 'Pathologische Mycologie,' and others), considered these changes as due to involution. I have already, in the 'Report of the Medical Officer of the Local Government Board, 1889–90,' and 'Centralblatt f. Bakt. und Parasitenkunde,' vol. vii, 1890, shown that this view cannot be correct, for the following reasons:

(*a*) In the diphtheritic membrane, in which the progress of the disease is still active, an abundance of diphtheria bacilli occur, which show this change in a marked degree, viz. segregation of the protoplasm into spherical, cubical, or cylindrical particles, and terminal knobs or clubs, sometimes of great size and containing vacuoles.

(*b*) On agar cultures, already after twenty-four to thirty-six hours, when the growth is in its initial and most active phase, an abundance of bacilli are seen, which are shorter or longer threads, in which the segregation of the protoplasm and the terminal knobs and clubs are already very marked (fig. 4).

(*c*) In the subcutaneous necrotic tumour of the cow, produced by subcutaneous injection of virulent culture of the Bacillus diphtheriæ, there occur connected masses and clumps in which at the growing margin the diphtheria bacilli appear all in the form of threads, in which the spherical or oval swellings and terminal knobs are most conspicuous, and strikingly resemble the ends of growing hyphæ; the subjacent muscular fibres become invaded and gradually destroyed by the growth of the threads into their substance. This process of the gradual growth and penetration of the diphtheria threads with swellings and club-shaped ends into the muscular

fibres is very marked, and occurs in a large number of places. It was described and illustrated in the 'Report of the Medical Officer of the Local Government Board, 1889–90,' pp. 173 and 174, plates xiv, xv, and xvi; and I have to add here that sections of the tumour stained in a mixture of eosin and methyl blue show this in beautiful contrast, the growing threads blue, the muscular substance red; and it seems to me that one has only to examine such a specimen to at once see that the threads are actively growing; of an involution there can be no question.

Dr. Abbott, in the 'Journal of Pathology and Bacteriology,' vol. ii, while agreeing that the thread-like bacilli with terminal swellings are not involution forms, and are present in the growing artificial cultures (on serum), does not agree to their being comparable to the growing ends of hyphæ. This difference seems, however, merely a question of words; all that I maintained was that the threads with knobbed ends strongly resemble growing ends of hyphæ, and that such a change in bacilli as I described in artificial cultures, and particularly in the growing threads in the cow's tumour, if it is not due to involution, as it certainly is not, is only explained by its representing a relationship to a mycelial fungus, perhaps the Saccharomyces mycoderma or an Oidium form.

(*d*) From the milk of cows successfully inoculated with cultures of the diphtheria bacilli (Report, 1889–90 and 1890–91) I have isolated by culture the diphtheria bacillus, and in the gelatine cultures they showed this change in a conspicuous manner; the colonies in their young state are almost entirely made up of thread-like forms with terminal knob-like and club-shaped swellings (figs. 5 and 6) quite unlike the typical bacilli. Here the bacilli are actively growing, and therefore it is quite out of place to regard these forms as due to involution; and if they are not involutions, their similarity in growth and shape strongly suggests the view that I have put forward, viz. that they are comparable to the hyphæ of a mycelial fungus, e.g. Saccharomyces mycoderma. In these threads with local accumulations of their substance, and with terminal knob-like or club-shaped enlargement of their proto-

plasm, we have a condition of things which does not harmonise with the fundamental characters of a typical bacillus, but rather suggests that this microbe, though under many conditions conforming with what corresponds to a typical bacillus, may after all not be one, or at any rate the boundary between it and a mycelial fungus is not a severe one.

C. The most instructive organism, showing a similar and perhaps more pronounced morphological change, is the tubercle bacillus of Koch. As is well known, this microbe presents itself in the tubercular deposits and in serum and agar glycerine cultures in a form which has vindicated to itself the term of a typical cylindrical bacillus. But already in preparations made of the human pulmonary (tubercular) sputum forms occur which appear more of the character of threads composed of unequal—i. e. not uniform—elements; some of these threads show not unfrequently a terminal element of the same knob-shaped or club-shaped character as those mentioned of the diphtheria bacilli. It was on account of such forms that Metschnikoff expressed the opinion that perhaps the tubercular bacillus is not a bacillus at all, but belongs to the group of mycelial fungi. I have already in 1889–90 shown that in glycerine agar cultures of the tubercle bacilli, after some weeks' growth at 37° C., there occur large numbers of such thread-like forms with club-shaped ends; some short, others long, some smooth, others made up of unequal elements; further, long and short threads occur which show undoubtedly and markedly branchings, these latter either of great length or only as just commencing sprouts (see figs. 7 and 8). That all these forms are undoubtedly the tubercle parasite is shown by the transitional forms between the typical cylindrical tubercle bacilli and the long-branched threads (homogeneous or segmented), with smaller or longer lateral buddings, and by the fact that all these forms behave in staining (fuchsin, washing with nitric acid, 1 : 3) like the true tubercle bacilli. I have seen the same forms already after three to five weeks' growth on solidified hydrocele fluid; here most of the organisms were the typical cylindrical bacilli, but there were some undoubted

threads with knobbed ends, some branched, others as yet unbranched.

There can be no question about involution, because, as I have pointed out (l. c., and 'Centralblatt f. Bakteriology,' vol. vii, No. 25), the branched nature of the threads and the presence of the small lateral buddings conclusively prove the active growth. Later, Mafucci ('Archiv f. Hygiene und Infect.,' xi, p. 445) described the same forms in the culture of the tubercle bacilli of the fowl, and Fischel ('Fortschr. d. Med.,' Bnd. x, No. 22, p. 908) also of the human tubercle cultures; and this latter observer arrived at the same conclusion as myself, viz. that we are dealing with forms which are comparable to a mycelial fungus.

From all these facts I think we are justified in concluding that the above three species are not so well-marked typical bacilli as has always been assumed; that is to say, well-defined species of desmo-bacteria in the sense of F. Cohn. True, under many conditions they show morphological characters of the same kind as the typical bacilli; but under other conditions they easily revert to or assume forms by which their relation to the Saccharomyces or Oidium (anthrax, diphtheria), or a still higher mycelial fungus (tubercle) becomes evident.

EXPLANATION OF PLATE 1,

Illustrating Dr. E. Klein's paper, "A Contribution to the Morphology of Bacteria."

All figures are reproductions from photograms magnified 1000.

Fig. 1.—Cover-glass specimen of Bacillus anthracis growing in gelatine plate, two days old. Many of the bacilli are changed into spherical or oval masses, containing vacuoles.

Fig. 2.—Cover-glass specimen from an impression of a gelatine-plate cultivation of Bacillus anthracis, two days' growth. Instead of the typical threads of cylindrical bacilli, there are threads made up of thick spindles, the protoplasm in many of these vacuolated.

Fig. 3.—From the same plate cultivation as the previous figure. Copious vacuolation.

Fig. 4.—From an agar culture of the Bacillus diphtheriæ, grown at 37° C. for two days, showing typical club-shaped filamentous bacilli.

Figs. 5 and 6.—Diphtheria bacilli, derived from the milk of a cow infected with diphtheria. The bacilli had been growing on gelatine. Typical club-shaped filamentous forms.

Figs. 7 and 8.—From glycerine-agar cultivations of the tubercle bacilli. Filamentous bacilli with terminal knob-like enlargements, some showing distinct branching.

On Certain Points in the Development and Anatomy of some Earthworms.

By

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Professor of Biology in the Presidency College, Madras.

With Plates 2—5.

The following notes are selected from a more extended series of observations which I am making upon this subject, and would not have been published separately, but that I wished to take this opportunity of testifying to my regard for one who has been for so long, and still is, my teacher and friend.

Much of the literature of the subject has not yet reached me (including the later portions of Vejdovsky's 'Entwickelungsgeschichtliche Untersuchungen'), and I have been obliged to defer any detailed reference to it until a future occasion. The organs dealt with are the setæ and the nephridia, and I have added a synoptical description of the two new species of worms with which the paper chiefly deals.

New Species.

The two worms, Mahbenus imperatrix and "Perichæta" pellucida, both belong to the family Perichætidæ, but neither of them to the genus Perichæta. For the one I have founded a new genus, being fairly confident as to what constitute its generic characters; for the other I have abstained from so doing, as it is, I think, allied to some of the new species described by Fletcher, while it is the only representative of the

genus which I have come across. I speak of it for the present as Perichæta.

Mahbenus, gen. nov.

Setæ very numerous. Circles of setæ almost continuous.

Clitellum extends over more than three segments.

Male pores, one pair, very close together, no setæ between the male pores.

Gizzard occupies not more than one segment.

Intestinal cæca absent.

Septa normal.

Micronephridia present.

Testes, two pairs, freely exposed.

M. imperatrix, sp. nov.

Length 650 mm. Circumference 35 mm.

Segments 200.

Colour rich dark brown, lighter on the ventral surface.

Prostomium encroaches very slightly upon the peristomium.

Setæ.—Segment II, 52; Segment V, 80; Segment IX, 110; no modified setæ; setæ remain in the clitellum. The circles of setæ are continuous in Segments II—XVII and XIX, the circle is interrupted ventrally in XVIII by about eight seta gaps, and in all the posterior segments there is a tiny gap recognisable only with care in the median dorsal and ventral lines.

Clitellum not strictly confined to particular segments, may extend over Segments XIV—XIX and part of XX.

Genital Apertures.—Male pores very small and quite close together (with not much more than a seta gap between them); the region immediately around them becomes raised into an oval papilla after killing in spirit. Two pairs of glands open in the region of the male pores, one pair on Segment XVII behind the circle of setæ, and one pair between Segments XIX and XX; their apertures lie about as lateral as seta 6.

The oviducal apertures are paired.

The spermathecal apertures are very small, and placed

between Segments VI-VII, VII-VIII, and VIII-IX; the two pores of each pair are remarkably close together, so close as to be only recognisable with care as separate apertures.

Dorsal Pores.—The most anterior dorsal pore lies between Segments V and VI; they are present in the clitellar region in the young worm, but become completely obscured when the clitellum is developed.

Alimentary Tract.—The gizzard is in Segment VII; dilated portions of the œsophagus serve as calciferous glands in Segments IX to XV; they are large in Segments XI to XIV only.

The typhlosole is a simple flap, deep, down to about Segment LXIV; there it narrows, becomes a mere ridge, and goes on to Segment CXVIII, and there ends abruptly, and at the same place the alimentary epithelium changes and becomes rectal.

Vascular System.—The dorsal vessel is double in Segment VII and onwards for a considerable distance.

Nephridia.—Minute micronephridia are present in large numbers.

Generative System.—The testes lie in Segments X and XI, and are attached to the septa bounding these segments anteriorly. The ciliated rosettes lie in the usual position. Prostates are large and rounded, and are provided with a muscular duct. The seminal reservoirs lie in Segments IX and XII. The spermathecæ are sausage-shaped sacs with a short duct, and a small cæcum lying in the thickness of the body-wall, and, what is very unusual, increase in size from before backwards. A spermatheca of Segment IX is more than three times as long as one of Segment VII. The ovaries and oviducts lie in the usual positions.

Perichæta pellucida, sp. nov.

Length 450 mm. Circumference 12 mm.

Colour.—The body-wall is very transparent, so that the colouring depends on the blood and the contents of the alimentary canal.

Prostomium small, not dovetailed into the peristomium.

Setæ.—Segment II, 24; V, 44; IX, 36; XX, 36. The number is subject to variations, and they are not very regularly arranged. No modified setæ are present. The dorsal gap is equivalent to about ten seta gaps, and the ventral gap to about three or less.

Clitellum not strictly confined to particular segments; it extends over Segments XIII—XVIII and a little into Segment XII. The dorsal pore XII-XIII lies well within the clitellum, and posteriorly it extends nearly up to the seta ring of Segment XX. It is not well developed in the ventral region.

Genital Apertures.—The male pores lie in Segment XVIII and thus in the clitellar region, although the clitellum is not developed in their neighbourhood. They lie in a small dumb-bell-shaped pit in preserved specimens. The distance between them is equivalent to about five seta gaps. There are no setæ between them. There are no other apertures in this region.

The oviducal apertures are paired, and lie about in the direction of seta 1, and just in front of the seta ring in Segment XIV.

The spermathecal apertures are placed between Segments VII-VIII and VIII-IX, and in the direction between seta 1 and seta 2.

Dorsal Pores.—The most anterior dorsal pore lies between Segments V and VI. They remain obvious between the clitellar segments.

Alimentary Tract.—Gizzard is in Segment V.

The œsophagus presents dilatations with vascular walls in Segments VI to XIII. There are well-developed calciferous glands in XIV, XV, and XVI. Saccular intestine commences in Segment XVIII.

There are no intestinal cæca.

There is no typhlosole.

Nephridia.—There is a pair of complex (see below) nephridia in each of Segments VII to XI, and a pair of small simple nephridia in each of the following segments. There are no micronephridia.

Generative System.—Testes lie in Segments X and XI,

and are attached to the septa bounding these segments anteriorly. The ciliated rosettes lie in the usual position. The prostates are long tubular-shaped glands, but remain in Segment XVIII.

The spermathecæ are elongated pyriform sacs with a small cæcum.

The ovaries and oviducts lie in the usual positions.

Setæ.

The setæ which first develop are, in all the worms which I have studied, replaced by others in either all or in the greater number of the segments before the embryo leaves the capsule; the replacement takes place in regular order from before backwards, and if it has not taken place in the hindermost segments before birth it does so shortly after. I speak of the setæ which first develop as embryonic setæ, and of the setæ which replace them as permanent setæ, although, of course, these may drop out and be again replaced later. The groups of cells from which the embryonic setæ of any segment develop I term secondary setal matrices. The secondary setal matrices develop from a primary setal matrix in each segment on each side of the body whether the complete number of setæ in the segment is four on each side or a larger number, as in the Perichætidæ.

Origin of the Primary Setal Matrices.

To exemplify this I have taken figs. 1—8 from sections of an embryo of Mahbenus imperatrix. The embryo was the same as that drawn in fig. 33, and was 7 mm. long when removed from the capsule. The sections were cut longitudinally through the tail end after it had been flattened out as in fig. 33. They are ·006 mm. thick. They were drawn with a camera lucida and Zeiss F, oc. 3 (for figs. 1—6; oc. 2 for figs. 7, 8), and as drawn are, therefore, magnified about 1100 diameters. The indentation marked x in figs. 1—3, due to a fold caused by the flattening, serves to mark the relative

antero-posterior position of those three sections. Fig. 1 passes through the "primary mesoblast" of the right side; the next section on one side (not figured) is preçisely median and passes between the "mesoblasts," while the section beyond (not figured) passes through the "mesoblast" of the left side. Fig. 2 is the next section to the right of fig. 1, and fig. 3 the next beyond; they show the row of cells proceeding from the "mesoblast" of fig. 1 passing slightly outwards and forwards (cf. fig. 33). Fig. 4 is a portion of the section next to fig. 3, and commences about half its own length beyond where fig. 3 leaves off; it shows the row of cells proceeding from the neuroblast of the right side. The lines *A B* in figs. 4, 5, and 6 are drawn at the same level to show the relative antero-posterior positions of the figures. Fig. 5 is the seventh section from fig. 1, but the cells *a*, *b*, and *c* are inserted from the eighth and ninth sections, while fig. 6 is the tenth section and the most lateral of the series.

Figs. 5 and 6 show the origin of the primary setal matrices; they arise on each side from a longitudinal row of cells which is, I have little doubt, the row arising from Wilson's lateral teloblasts.[1] These cells, at first very superficial, take up as they pass forwards a deep-lying position within the cœlom. At first there is one cell on each side in each segment lying close to the nephridial cell (fig. 5). Their further history is shown in figs. 7 and 8; fig. 8 comes from near the median line a little in front of fig. 4, and includes a portion of the nerve-cord; fig. 7 lies a little behind and to one side of fig. 8. The setal matrices are now seen to consist of several cells. There is not the slightest difficulty in tracing these structures forwards from segment to segment until they are old enough to have developed setæ.

The embryos of Moniligaster (probably M. sapphirinaoides) which I have in these early stages show also very clearly that the primary setal matrices take their origin from continuous longitudinal rows of cells, but neither here nor in Mahbenus, at any rate in the youngest stages which I have examined, are

[1] 'Journal of Morphology,' vol. i, 1887.

any of the teloblasts except the "mesoblasts" as specially enlarged as they are in Lumbricus.

I gather from Bergh ('Zeit. f. w. Zool.,' Bd. 1, p. 523) that Wilson has, in a paper which I have unfortunately been unable to see, shown that "the outer setigerous glands arise from the lateral cell-cord," and that he recognises a "setiblast." My observations, which were originally made without any knowledge of the previous literature, corroborate Wilson's, but go further, as I show that all the setal matrices, however many there may be, arise on each side of the body as a cell-cord. My observations on the development of other organs are still very incomplete, but so far as they go they have led me to the conclusion that all the organs which express a metameric segmentation arise from the cords of cells which grow forwards in the germ bands. The mesoblastic bands give rise, I believe, to the muscles of the septa and cœlomic epithelium and blood-vessels only, while the muscles of the body-wall which do not exhibit metamerism arise in some other way. I find no evidence that they arise directly from epiblast, but a certain amount that they arise at an early stage from the primary mesoblasts, and perhaps also from the mesoblastic cords before these have become segmented, growing outwards in all directions, and not in that direction alone which is taken by the mesoblastic cords. Certain it is that at a time when the germ bands are still in their infancy muscles are to be found underlying the whole of the epiblast. Besides the muscles of the body-wall, the epidermis, and the alimentary tract, the only other organs which do not arise from the germ bands exhibit no metamerism in the embryo. The occurrence of such organs as the gizzard in such varying segments in different worms would be explained if we can show that what segmentation the alimentary tract possesses has nothing to do with the metameric repetition of other organs. I have further, like Bergh, come to the conclusion that the nerve-cord arises from two distinct matrices, and that the ganglia are the only structures which arise from the neuroblastic cords. The above theory will, I foresee, land us in great difficulties when we consider organisms other than worms,

and I put it forward with great diffidence and in a purely tentative manner.

Development of the Secondary Setal Matrices.

The primary setal matrices grow in each segment laterally, and also to a lesser degree towards the ventral median line, as soon as they have taken up their position in the cœlom and become covered by cœlomic epithelium.

The primary matricial cells become segregated to form the secondary matrices. The number of these formed in each segment varies; in Moniligaster each seta couple arises from a single matrix, which accounts for the fact that the two setæ of the couple are always so close together. This is also the case in Lumbricus.

In Acanthodrilus sp. the setæ are slightly "separated," and each seta develops from a separate secondary matrix. In Urochæta there may be three or two secondary matrices on either side, according as the setæ are "scattered" or not in a particular segment on that side (fig. 16). The exact arrangement which obtains in regard to this matter in "Perichæta" pellucida is described below, but, speaking generally, in this form and in M. imperatrix and in Perionyx saltans each seta arises from a separate secondary matrix.

All the secondary matrices on each side of the body remain connected together for a longer or shorter time by a band of tissue which stands out freely into the body-cavity, and is composed of the cœlomic epithelium cells which covered the primary matricial cells as they grew out to form the secondary matrices, and may be termed the intermatricial band (figs. 20, 24, &c., *im.*; cf. Vejdovsky, 'Entwickelungsgeschichtliche Untersuchungen,' Heft 3, Tab. xxiii, fig. 19, *i. f.*, and Tab. xxviii, fig. 7, *im.*).

Fig. 9 is a portion of an embryo of Moniligaster flattened out, drawn with a camera lucida and Zeiss BB, oc. 3, magnified about 150 diameters. At *p. m.* is seen a series of primary setal matrices, the more anterior ones commencing to grow outwards; in the four segments (*im.*) the formation of the two

secondary matrices is taking place, these being connected by the intermatricial band. This band disappears very early in Moniligaster, and in the anterior segments are seen inner and outer secondary matrices, as at *s. m. i.* and *s. m. o.* In the most anterior segment drawn, a seta (*set.*) is appearing in the inner secondary matrix. The embryo from which this figure is drawn has about fifty segments in front of those drawn, but it is not possible to count any segments behind those drawn, i. e. they are not distinguishable as segments in such a preparation; longitudinal sections enable one to count them further back.

Figs. 10—13 show the development of the secondary matrices in Moniligaster studied in sections. They are taken from a series cut transversely through a portion of an embryo of about the same age as fig. 9, and which had been flattened out in the same manner. They represent the matrices of four consecutive segments; three or four sections are omitted between those figured. The upper part of each figure lies near the nerve-cord. They are drawn with a camera lucida to the same scale as figs. 1—7. Figs. 10 and 11 show primary matrices, that in fig. 11 projecting freely into the cœlom, while that in fig. 10 does not; and in these segments there is quite clearly no other setal matrix on either side of the nerve-cord. In the next segment in front, the primary matrix has given rise to two secondary matrices on each side, those of one side being shown in fig. 12; four inches of the drawing have been cut out in the middle to place it upon the plate. In the next segment in front, the inner and outer secondary matrices are quite separated from one another; the inner one alone is figured. The epidermic thickening marked *x* is one of a series of such structures with regard to which I can at present give no further information. I figure it to show that it is not a "seta follicle." Fig. 14 is a surface view of a secondary matrix, showing the development of the seta couple (*set., set.*); the cœlomic epithelium shown all round is omitted from the surface of the matrix. Fig. 15 shows in a slightly older stage, from a longitudinal section, one of the setæ of a couple.

Fig. 16 shows in a diagrammatic manner a late stage in the development of the secondary matrices in Urochæta. In all the five segments figured, except the most posterior, the primary matrix has completely separated into two secondary matrices. In the segments marked *a* and *c* the outer secondary matrix is further dividing into two to place seta 4 in the very dorsal position it occupies in alternate segments.

The investigation of the development of the secondary setal matrices from the primary ones in the Perichætes is attended with great difficulties. To work out the question thoroughly satisfactorily it would be necessary to obtain a series of very thin sections, so accurately transverse to the long axis of the embryo that in each segment one section passed through the whole of the region of the future seta ring. No amount of care would with certainty secure such a series, and my efforts in this direction have not been attended with any special luck. I have, however, sufficient evidence to prove that the only important difference in this respect between the Perichætes and Moniligaster is in the number of secondary matrices which are produced. In the preparation shown in fig. 33, from the tail end of which the sections (figs. 1—8) that show the origin of the primary matrices were obtained, these primary matrices may be traced growing gradually outwards; older embryos show that they do this until they have grown right round the segment on each side. The cells meanwhile segregate to form the secondary matrices, the segregation commencing at the ventral ends of the matricial bands, and proceeding gradually towards the dorsal region.

The later stages in the process of production of the secondary matrices I have most conveniently studied in Perichæta pellucida, but the small size of the embryo prevented my seeing the earlier stages in that form. I think we may fairly assume, considering the close agreement that obtains between two such different forms as a Moniligaster and Mahbenus imperatrix, that the origin of the primary matrices and the proliferation of their cells to give rise to secondary matrices takes place as in those forms. The production of the secondary

matrices in P. pellucida does not, however, take place in regular succession, beginning at the ventral and ending at the dorsal end of the band. It is quite clear that in P. pellucida new secondary matrices are produced between existing ones, either by matricial cells which separate from the existing matrices and travel along the intermatricial band, or by the division of any matrix into two. There is obviously no essential difference between these two methods, nor is it possible to draw any definite line of demarcation between them, but the latter method prevails in the earlier and the former in the later stages of the production of the full number of secondary matrices.

Fig. 17, from a transverse section of an embryo of P. pellucida, shows a secondary matrix dividing into two. Fig. 18, from the same series, shows two secondary matrices connected by the intermatricial band; one of these is the most ventral of the series belonging to one side of a segment, while the other one shows the band connecting it with the next matrix beyond.

Figs. 19—25 are views of portions of matricial bands of embryos of P. pellucida which had been slit open and flattened out; they are arranged, with the exception of fig. 23, in the order of their age. Fig. 22 shows the entire matricial bands on one side of three consecutive segments.

In P. pellucida the two secondary matrices first produced from a primary matrix come to lie at the two ends of an entire band, all the other matrices in the band being subsequently produced. I have deduced this law from the order of appearance of the setæ, assuming, as we fairly may, that the matrices form these setæ on arriving at similar ages.

When all the secondary matrices have been developed they come to lie at nearly equal intervals from one another, and the intermatricial band gradually disappears (fig. 25).

Development of the Embryonic Setæ.

In this, as in all other matters relating to the segmentally arranged organs, any segment presents during development

a slightly further advanced condition than the segment behind it.

I have studied the order of development of the embryonic setæ in a very large number of embryos of P. pellucida, and figs. 26—28 are given as three typical stages; they are diagrammatic, but accurate in respect of the number of setæ present. The embryo is supposed to have been slit open and flattened, and all the setæ on one side of the body are shown. *V. V.* and *D. D.* represent the median, ventral, and dorsal lines.

These figures show that the setæ develop, as a rule, in couples, that the most ventral couple is the earliest to develop, that the couple which become the most dorsal follow next, and that then with considerable regularity ventral and dorsal couples appear alternately; further that from a very early stage the appearance of the setæ becomes retarded in Segment II, a retardation which afterwards extends to the next two or three segments (in stages later than those figured).

All the setæ in figs. 26—28 are embryonic setæ, no permanent having yet appeared even in fig. 28.

In Mahbenus and in Perionyx the order in which the setæ appear is different; the most ventral appear first, then those next to them, and so on, the most dorsal appearing last. I expect that this represents a more modified condition; in P. pellucida each segment passes in the condition of its setæ through a stage which remains as the permanent condition in an octochætous form.

In Moniligaster, Acanthodrilus, and Lumbricus the earliest seta to develop on each side in each segment is the seta which becomes seta 1 (i.e. the most ventral), the next to develop is seta 4, the next seta 2, and then seta 3.

Adult Condition and Formation of the Permanent Setæ.—The setæ in the adult P. pellucida in any segment lie at irregular intervals from one another, and the number of the setæ in a ring varies to a small extent. The actual number of setæ in a particular specimen lying on one side of the body in Segments XXV—XXVII are shown in fig. 29, the relative distance between one seta and another is accurately shown,

but the setæ themselves are magnified. It is very rare in the adults of this species to find young setæ ready to replace old ones which drop out, and I believe that the setæ shown in this figure were the "permanent" setæ formed in the embryo. I term them permanent setæ in contradistinction to the embryonic setæ which precede them. The permanent setæ develop at regular intervals from one another, except for the dorsal and ventral gaps, and a greater number are formed than occur in the adult, so that some drop out, leaving those which remain at irregular intervals from one another. The number of those that drop out appears to be nearly constant.

The permanent setæ begin to appear on either side of the dorsal and ventral median lines, one in the immediate neighbourhood of each embryonic seta (fig. 30); the last to appear are the most laterally placed ones. If 50 setæ develop in the ring (the largest number I have found in this species) seta 1 develops first, then seta 25 on each side, then in fairly regular order, 2, 24, 3, 23, and so on. They always develop first in the most anterior seta-bearing segment (II), and then very regularly backwards. They always begin to appear before the embryonic setæ are visible in the most posterior segments. I give three examples:

1. Embryo 25 mm. long, 160 segments counted, with a growing tail in which the segments could not be counted when mounted whole, embryonic setæ visible down to Segment LXV, but mere dots after XXX, and four pairs only present in the hindermost of the segments in which setæ are already visible (say LV to LXV); the permanent setæ are just beginning to develop, and are visible in Segments II—V (see fig. 31).

2. Embryo 30 mm. long, embryonic setæ visible down to Segment CIII, the number of embryonic and permanent setæ in the anterior segments are as under:

	Embryonic setæ.	Permanent setæ.
Segment II	6	35
,, III	12	40
,, IV	19	40
,, V	28	50
,, VI	38	36
,, VII	39	27
,, VIII	40	26
,, IX	48	12
,, X	52	2
,, XI	44	0

The seta rings of Segments II, III, and IV of this worm are shown in fig. 32.

3. Embryo 40 mm., embryonic setæ down to CLXXXVI, the number of embryonic and permanent setæ as under:

	Embryonic setæ.	Permanent setæ.
Segment II	18	32
,, III	25	42
,, IV	40	48
,, V	30	32
,, VI, VII, VIII, IX	40 to 50	few and very small
,, X and onwards		none

This embryo was much more backward in regard to its seta development; it had not lost so many embryonic setæ nor developed permanent setæ to such an extent as had the others.

Nephridia.

Development of the Nephridia in Mahbenus imperatrix.

I propose to deal here with certain stages only in the development of these organs—the stages which have a special bearing upon the so-called "plectonephric" condition. I deal chiefly with Mahbenus imperatrix. All my observations on the early stages corroborate those of Vejdovsky, and the later

stages now described resemble very closely those described by that author in dealing with Megascolides australis ('Archiv für mikr. Anat.,' Bd. xl).

In an embryo such as that from which figs. 5—8 and 33 are taken it is quite clear that the nephridia arise as paired structures, a pair in every segment except perhaps the first. Nephridia 7 and 16—19, from the right-hand side of this embryo, are shown enlarged in figs. 34, 35.

Each consists of a præseptal funnel, a neck connecting the funnel with the glandular loop, and an excretory duct.

The funnel is at no stage well developed, and is probably never functional, and afterwards entirely degenerates.

This neck becomes afterwards a very important structure, and is dealt with below.

The glandular loop arises by budding from the neck region and rapidly enlarges, ductules develop within it, and it becomes a very complicated structure, as shown in fig. 35 and in outline in fig. 39. It certainly corresponds to a macronephridium of Megascolides, but its further development becomes arrested, and I have been unable to distinguish it in the adult from the loops of the micronephridia which subsequently appear.

It is important to note that owing to the imperfect state of development of the septa these loops are by no means confined to their own segments.

The excretory duct also arises from the neck region as a solid outgrowth (fig. 34, *neph.* 17; and fig. 37, *ex. d.*); it very soon acquires a lumen and opens to the exterior. It elongates rapidly, more than keeping pace with the body-wall in its growth, and the aperture comes to lie very dorsally; the excretory pores of all the nephridia in front of nephridium 17 lie outside the preparation in fig. 33.

The series figs. 36—39, taken from an older embryo, traces the further development of the nephridia; the figures represent the 7th, 55th, 75th, and 86th nephridia respectively. Fig. 39 represents, therefore, a later stage in the development of the nephridium of fig. 35, but figs. 36—38 represent stages in the development of nephridia which did not exist in the embryo of

fig. 33, and show that the mode of development alters in the nephridia which are late in appearing.

I have been unable, owing to the advanced stage of development of all the other structures, to fully trace out the nephridium of fig. 39; but there is sufficient to show that the neck has undergone great elongation, so that the glandular loop lies very dorsally. The loop itself has become very complicated, and the excretory duct extends away beyond the portion drawn. The great importance of the stage is that it shows the developments which are taking place in the neck region. The cells here are giving rise to the secondary loops (*n.* 1, *n.* 2, *n.* 3).

Fig. 38 shows that in a nephridium developing at this late stage the growth in the neck region commences at a relatively much earlier stage. The neck is here already much elongated, while the primary loop is still very undeveloped and the excretory duct has not yet acquired its proper lumen. It is clear that the primary loop is the earliest to develop of a series, and that the whole structure is the homologue of the nephridium of Lumbricus, and, as these secondary loops form or give rise to all the scattered nephridia on the one side of each segment, these are taken as a group, but not individually, homologous with the Lumbricus nephridium.

Fig. 40 is taken from an old embryo; *n n* is a portion of the original neck region, now much attenuated; *a* to *f* are secondary loops which have arisen from it; of these *a*, at any rate, has acquired an excretory pore. These loops show that the same sort of difference obtains between a secondary loop which develops late and one which develops early as between a nephridium which develops late and one which develops early.

The secondary loops give rise to tertiary loops as outgrowths from their own neck region. In this way some fifty or more loops develop which ultimately become separated from one another, while each develops its own excretory duct and becomes a micronephridium.

There is no elongation in the neck region and no development of secondary loops in the nephridia of the most anterior

segments; the whole structure aborts in these segments, so that in the adult no nephridia occur in them.

I find absolutely no trace of provisional nephridia from a gastrula stage onwards, though, of course, in a sense all the loops which first develop are provisional, and I expect that all so-called provisional nephridia will be ultimately explained by the fact that the mode of development and ultimate structure, and even continued existence of a nephridium, depends upon its time of development; and, further, that the nephridia which develop early are not confined by septa to their own segments. This becomes very clear in large embryos like those of Mahbenus.

Fig. 41 shows as much of the anatomy of a micronephridium of an adult as I have been able to make out; the whole structure as drawn is 0·25 mm. long.

Development of the Nephridia in some other Worms.

In P. pellucida the nephridia develop in the same way as in Mahbenus, certain details excepted, as that the funnel becomes better developed up to a certain stage, up to such a stage as fig. 35. The loop has then the same long wandering character. At this stage all resemblance ends. The loop becomes broader in proportion to its length, no elongation occurs in the neck, no secondary loops are formed, and each segment in the adult never possesses more than a single pair of nephridia. The five most anterior pairs, after having attained a well-developed condition, degenerate and entirely disappear. The most anterior pair of nephridia in the adult belong to Segment VII.

The nephridia of Segments VII—XI undergo further modification until their structure somewhat resembles that of the nephridia described by Benham in Microchæta. From a portion of the ordinary loop a number of outgrowths form, into which the tubules run in a very complicated manner, and this bunch of outgrowths ultimately form by far the largest portion of the nephridium.

Fig. 42 is taken from a fortunate preparation obtained by

macerating a portion of a full-sized embryo in nitric acid. I found it impossible to make out all the details. At *d.* is seen the excretory duct, composed of a very regularly arranged series of drain-pipe cells; *b.* is the apex of the lobe; at *c.* the arrangement of the tubules is very characteristic,—there is a central tubule and a double set of convoluted tubules, shown in the figure by single lines; at *a.* is the bunch of outgrowths, each one of which subsequently elongates to a considerable extent.

In a Madras species of Acanthodrilus which has scattered nephridia in the adult I have found the nephridia to develop as paired organs, one pair to each segment, which bears out Beddard's observations upon this genus (this Journal, vol. xxxiii, part 4). I have inserted fig. 43 of the 17th nephridium from a 10 mm. long embryo of this species, as it showed with absolute clearness the exact course of the greater portion of the ductule from the excretory duct *d.* up to *b.*; from thence onwards to the funnel duct the ductule was too fine to be traced. I have not yet obtained stages of this species showing the development of the micronephridia, but as the process seems to be so similar in such widely different forms as Mahbenus imperatrix and Megascolides australis it is probably the way in which all micronephridia develop.

The So-called "Plectonephric" Condition.

My own observations, those of Vejdovsky, and in a less direct way those of Bergh, Wilson, and others who have dealt with development of the nephridia in meganephric forms, and even those of Beddard himself (on the development of A. multiporus), throw grave doubt upon the conclusions arrived at by Beddard and Spencer with regard to this matter. Apart from this I have for some years, upon anatomical grounds, doubted the existence even, of such a condition of the nephridium as was described by Beddard for P. aspergillum. For one thing, Beddard's figs. 7 and 10 (this Journal, vol. xxviii, Pl. XXX) do not seem to me to prove what he would have them prove; fig. 10 contains an impossible blood-vessel, branching and returning blood into itself, which looks very

much as though there had been some confusion between nephridial tubule and blood-capillary, while fig. 7 hardly shows a continuity of nephridial tubule from segment to segment. Further, both Beddard's and Spencer's figures, especially the latter, clearly show that the tubules possess a different character in different regions, and that they are therefore much more specialised than the tubules of Pontobdella; and in no case can one be certain of the continuity of such fine tubules from an examination of sections alone.

For my own part, (1) in spite of repeated and most careful search in preparations from so-called plectonephric worms made in all sorts of ways, I have never seen any connection between one nephridium and another in the adult. If, however, the mode of formation of the micronephridia is always such as I describe for Mahbenus, it is very possible that there are forms in which all or any of the micronephridia on the same side of any segment may remain connected together; but I very much doubt whether there is ever any continuity from side to side or from segment to segment.

(2) I have in a large worm like Mahbenus imperatrix been able to count the micronephridia belonging to a definite area, and then to mount the cuticle which showed a corresponding number of pores.

(3) The micronephridia have always a complicated structure, similar to that of a meganephridium. This is the fact which first led me to doubt the plectonephric condition, and I have worked out with great trouble as much of the structure of a micronephridium as is shown in fig. 44. This nephridium belongs to Perichæta mirabilis. The micronephridia in this worm are very numerous, and have, or some of them at any rate have, funnels; these funnels are not præseptal, and present eight marginal cells, ciliated on their centrally directed faces and arranged in a horseshoe fashion, and one central cell, but no other cells. The funnel is only 0·05 mm. in diameter. The coils of tubule are shown in the figure. Fig. 41 shows a similar complicated condition for Mahbenus, and I have obtained similar results in all the micronephridia which I

have examined, so that even if they were all connected together into a network and did not develop, as they appear to do, we should have a condition very different from that of Pontobdella, and much more nearly connected with a meganephric condition.

(4) I knew that in Perichæta pellucida and some other species which, although not to be placed, strictly speaking, in the same genus as P. aspergillum, P. mirabilis, &c., are very closely allied forms, one pair only of nephridia were to be found in any segment, which rendered it, at any rate, unlikely that anything so fundamentally different from the meganephric condition as the plectonephric condition would occur. (The existence of Perichætes with meganephridia reopens the question of the systematic position of Perionyx.)

I think that the condition of the nephridium in Perichætes, Acanthodrilus, and many other genera must have arisen from the meganephric condition. That the funnel appears, as in Mahbenus and Megascolides, only to disappear, and that the loop which appears earliest in the nephridia which develop first and attains such great complication, only to be arrested in its development or even to abort, to set aside all other considerations, is very strong evidence that the development of micronephridia by budding from it, is a specialised condition.

Taking into account what we know of the development of the nephridia in other leeches and the presence of funnels (if M. Bolsius will allow me to call them so), so seemingly out of keeping with the rest of the nephridium in Pontobdella, I shall not be surprised to learn from a history of its development that that is by no means a primitive structure, and has possibly no genetic relationship with the tubules of Platyhelminths.

I am unable at present to bring forward any direct evidence as to the relationship between genital ducts and nephridia in earthworms, but I cannot refrain upon this occasion from pointing out that the demonstration of the fact that a so-called plectonephric condition is not a primitive one removes the strongest objection to the theory brought forward by Lankester in one of his earliest contributions to this Journal.

EXPLANATION OF PLATES 2—5,

Illustrating Professor A. G. Bourne's paper "On Certain Points in the Development and Anatomy of some Earthworms."

PLATE 2.

Figs. 1—8.—From Mahbenus imperatrix, fully described in the text.

Fig. 1. *M.*, *m.* Primary "mesoblasts." *Ep.* Epidermis. *al. ep.* Alimentary epithelium (the cells fully shown here and in Fig. 8, partially so only in Figs. 2—7). *Musc.* Cells which give rise to the muscle of the body-wall (their presence here at this stage will be discussed in a subsequent paper). *x.* marks a corresponding spot in Figs. 1—3.

Fig. 2. *M.* Row of cells growing from the primary "mesoblast." Other letters as before.

Fig. 3. Letters as before.

Fig. 4. N. Neuroblast. *n.* Cells forming nerve-cord. *Sept.* Septum. *Cœl. ep.* Cœlomic epithelium. The line A B in this and Figs. 5 and 6 marks a corresponding level. Other letters as before.

Fig. 5. *a, b, c.* Row of cells giving rise to primary setal matrices, as *s.*, *s.* *Neph.* Nephridial matrix.

Fig. 6. *s.* Continuation backwards of the row *a, b, c,* of the preceding figure. *Neph.* Nephridial matrices; the actual nephroblast does not come into this section.

Fig. 7. Letters as before.

Fig. 8. Letters as before.

PLATE 3.

Figs. 9—15.—Moniligaster (probably M. sapphirinaoides).

Fig. 9. Portion of an embryo flattened out. *Neph.* Young nephridia. *n.* Portion of the nerve-cord. *Sept.* Septa. *p. m.* Primary setal matrices. *i. m.* Secondary setal matrices in process of formation. *S. m. i.* and *S. m. o.* Inner and outer secondary setal matrix. *Set.* Rudiment of a seta. *x.* Series of large cells of unknown significance.

Figs. 10—13. Transverse sections, described in the text. *p. m.* Primary setal matrix. *S. m. i.* and *S. m. o.* Inner and outer secondary setal matrix. *Neph.* Nephridium. *Ep.* Epidermis. *x.* Epidermic ingrowth.

Fig. 14. Surface view of an advanced secondary setal matrix. *set.*, *set.* The two sétæ of a couple.

Fig. 15. Similar structure from a longitudinal section.

FIG. 16.—Urochæta sp. Secondary setal matrices of one side of the five segments *a—e.* v. v. Ventral median line. *Ant.* and *Post.* mark the anterior and posterior regions.

PLATE 4.

FIGS. 17—32.—Perichæta pellucida; Fig. 33. Mahbenus imperatrix.

Figs. 17—21. Secondary setal matrices dividing before the appearance of setæ. *S. m.* Secondary matrices. *i. m.* Intermatricial bands. *Cœl. ep.* Cœlomic epithelium. *ep.* Epidermis.

Fig. 22. Portions of the setal matrices of two consecutive segments with developing setæ. In the lower portion of the figure which is anterior two new setæ are shown developing between an older pair.

Fig. 23. The entire setal matrices on one side of the body in three consecutive segments. V. Ventral end. D. Dorsal end. Setæ are seen developing in the most ventral and most dorsal regions, the former being the elder.

Figs. 24 and 25. Later stages in the development of the secondary matrices.

Figs. 26—28. Diagrams showing the exact number of setæ on one side of the body in the segments marked II, III, IV, &c., in three embryos of different ages. V. V. and D. D. mark the ventral and dorsal median lines.

Fig. 29. A similar diagram taken from an adult worm.

Fig. 30. Portion of a matrix in which permanent setæ are beginning to develop alongside the embryonic setæ.

Fig. 31. The complete seta ring of Segment II of an embryo 25 mm. long. The long fine lines represent the embryonic setæ, the short thick lines the permanent ones.

Fig. 32. The complete seta rings of Segments II, III, and IV of an older embryo from which the embryonic setæ have nearly all dropped in these anterior segments; those left are shown by the small fine lines, of which there are 6, 12, and 19 in the different segments.

Fig. 33. An embryo of Mahbenus imperatrix showing the entire series of nephridia. The references *Neph.* 1, *Neph.* 2, &c., are connected with the excretory ducts; the excretory pores themselves are within the limits of the preparation in the case of nephridia 7 backwards. S. m. Setal matrices. *Sept.* Septa torn during the removal of the alimentary wall.

PLATE 5.

Figs. 34—41. Mahbenus imperatrix; Fig. 42. Perichæta pellucida; Fig. 43. Acanthodrilus sp.; Fig. 44. Perichæta mirabilis.

Figs 34 and 35. Enlarged views of some of the nephridia from the preparation, Fig. 33. Letters as before.

Figs. 36—39. Series of nephridia from an older embryo of Mahbenus. *fun.* Funnel. *NK.* Neck region. *l.* Glandular loop. *Ex. d.* Excretory duct. *n.* 1, *n.* 2, *n.* 3. Micronephridia beginning to develop.

Fig. 40. From a still older embryo. *n. n.* Portion of the neck region of a nephridium such as Fig. 39. *a*, *b*, *c*, *d*, *e*, *f.* Micronephridia developing from it. *g.* Micronephridium developing from *a.* *Ex. d.* Excretory duct. *Ex. p.* Excretory pore. *s. m.* Setal matrices. *i. m.* Intermatricial band.

Fig. 41. A micronephridium from an adult Mahbenus.

Fig. 42. A nephridium from one of the Segments VII—XI of a full-sized embryo of P. pellucida.

Fig. 43. A nephridium from an embryo of Acanthodrilus sp. *B. W.* Body-wall. *Sept.* Septum. *fun.* Funnel. *a.* Duct from funnel. From *b* to *d* the exact course of the duct is shown. *d* passes downwards to the excretory pore.

Fig. 44. A micronephridium from an adult Perichæta mirabilis. *fun.* Funnel (not præseptal). *Ex. d.* Excretory duct.

On the Law of Development commonly known as von Baer's Law; and on the Significance of Ancestral Rudiments in Embryonic Development.

By

Adam Sedgwick, M.A., F.R.S.

The generalisation commonly referred to as v. Baer's law is usually stated as follows:—Embryos of different members of the same group are more alike than the adults, and the resemblances are greater the younger the embryos examined. It appears to be pretty clear that v. Baer held some such view as this,[1] and there can be no doubt that it is a view which is largely taught at the present day.[2] In fact, I think it is safe to say that all zoologists are brought up with this view as one of the fundamental postulates of their science.

It will be the object of the following pages to show that this view is not in accordance with the facts of development. V. Baer based his view mainly upon the study of Vertebrate embryos; and it will be convenient for us, in criticising him, to begin with an examination of this group. We may also, in the first instance, follow v. Baer in another point, viz. in limiting ourselves to the consideration of embryos as opposed to larvæ. Embryonic development and larval development take place under entirely different conditions, and in order to obtain clear ideas they must be considered apart in treating

[1] Vide 'Ueber Entwickelungsgesch. d. Thiere,' part i, pp. 221, 223, and 224.

[2] Vide Darwin in 'Origin of Species,' p. 364, 6th ed.; and Balfour 'Comp. Embryology,' vol. i, p. 2.

this subject. They have not as a rule been clearly distinguished, and facts based on a study of larvæ have sometimes been assumed to hold true for embryos without further examination; and this practice has, as I hope to show, given rise to errors which have prevented our arriving at a clear understanding of the subject.

It is, of course, impossible to examine fully all the stages of all Vertebrate embryos. In the comparison necessary for the criticism I am making it will be convenient to limit ourselves to typical cases, and I propose to consider (1) the embryos of animals widely divergent ; (2) the embryos of animals which are closely allied in the adult state. If it is found that in neither of these cases is the law of v. Baer followed, then I think we may reason that there is, to say the least of it, a strong probability that it will be found not to hold true for intermediate cases.

(1) Embryos of divergent classes of the Craniate phylum. The examples I have chosen are the fowl and dog-fish.

The fowl and the dog-fish in the adult state live under entirely different conditions; whereas in the embryonic phases the conditions are very similar, both being developed within an egg-shell at the expense of ovarian yolk and surrounding albumen.

According to the law of v. Baer these embryos ought to be closely similar in the young stage.

Do these embryos, developing under similar conditions, conform to the law? Superficially, clearly not. There is no stage of development in which the unaided eye would fail to distinguish between them with ease—the green yolk of the one, the yellow yolk of the other; the embryonic rim and blastopore of the fish, the absence of these in the chick; the six large gill-slits bearing gills on the one hand, the four rudimentary clefts on the other; the small head, straight body, and long tail, as opposed to the enormous head, cerebral curvature, short tail, and so on. A blind man could distinguish between them.[1] These embryos are not closely similar,

[1] I do not feel called upon to characterise the accuracy of the drawings of

but it is maintained that the law is justified by certain remarkable features of embryonic similarity which the adults do not exhibit, and of which the most important are the presence in the chick of pharyngeal clefts, a tubular piscine heart, and a similarity in the arrangement of the cardiac arterial system, a cartilaginous endo-skeleton, oro-nasal grooves, and a notochord. Now I freely admit that these are striking similarities, but I question whether they are sufficient to justify the law of v. Baer. By themselves, no doubt, they would be sufficient to justify that law; but are there no differences to set off against them? Are there no differences of a morphological value, as far-reaching and as striking as these similarities? Let us clearly understand the question at issue. V. Baer's law, as applied to the present case, may fairly be held to mean, if it has any meaning at all, that whereas the differences between the adults are large and important differences of class value, the differences between the embryos are slighter and unimportant, and of less than class value. Now in no single member of the group Craniata is the mesoderm of the head segmented. According to our present morphological knowledge, the discovery of an animal with cranial segments would be a very remarkable one, and would, we might confidently predict, require the establishment of a class at least separate from all other Craniate classes—such is our estimation of the importance of this feature. And if to this character was also added the presence of a cœlomic sac close to the eye, of another in the jaw, and of a third near the ear; of an aperture of communication between the neural canal and rectum, of kidney tubules opening into the muscle-plate cœlom as well as into the perivisceral cœlom, of a Müllerian duct opening into the front end of the Wolffian, I do not think that any anatomist would have any doubt about the matter. Now it is precisely in these points, amongst

embryos of different classes of the Vertebrata given by Haeckel in his popular works, and reproduced by Romanes and, for all that I know, other popular exponents of the evolution theory. As a sample of their accuracy, I may refer the reader to the varied position of the auditory sac in the drawings of the younger embryos.

others, that the embryo dogfish differs from the embryo chick. I am quite aware that arguments tending to reduce the classificatory value of the embryonic differences I have just enumerated might with more or less plausibility be adduced. But one thing at a time. I am at present dealing solely with the importance of the anatomical resemblances and differences between the embryos; and I think I have shown, as far as it can be shown, that they have, if judged by standards used when comparing adults, at least as great an importance as the resemblances between the same embryos—the differences, like the resemblances, relating solely to the embryos, and not existing in the adults. V. Baer's law then falls to the ground, and must be replaced by another law, which is as follows:—Embryos of different members of the same group often resemble one another in points in which the adults differ, and differ from one another in points in which the adults resemble; and it is difficult, even if possible, to say whether the differences or the resemblances have the greater zoological value (because we have no clearly defined standard of zoological value).

It will probably be urged here by my reader—Are you not beating the air in a vain warfare of words and unessentials of which we were all aware, and trying to kick up a cloud of dust by which to obscure the essential point, viz. that embryos pass through, incompletely if you like, stages of structure permanent in lower members of the same group? To such a one I reply, that I am as keenly alive to the importance of the essential point as he is, but that I differ from him in being dissatisfied with the explanation which is at present given of it, and that I am convinced that the form in which this phenomenon is referred to in v. Baer's law has led to the acceptance of an imperfect explanation of the embryonic phase in animal development.

(2) But before I come to that point I have to consider the case of the embryos of closely allied animals. If v. Baer's law has any meaning at all, surely it must imply that animals so closely allied as the fowl and duck would be indistinguishable in the early stages of development; and that in

two species so closely similar that I was long in doubt whether they were distinct species, viz. Peripatus Capensis and Balfouri, it would be useless to look for embryonic differences: yet I can distinguish a fowl and a duck embryo on the second day by the inspection of a single transverse section through the trunk, and it was the embryonic differences between the Peripatuses which led me to establish without hesitation the two separate species. But it is not necessary to emphasise further these embryonic differences; every embryologist knows that they exist and could bring forward innumerable instances of them. I need only say with regard to them that a species is distinct and distinguishable from its allies from the very earliest stages all through the development, although these embryonic differences do not necessarily implicate the same organs as do the adult differences.

If I have laid great stress—some may think undue stress—upon the inadequacy of v. Baer's law, I have done so because of the importance which is at the present day attached to this law by teachers of zoology. In support of this, I may quote the words of three of the greatest teachers of zoology of this or of any other age—words which show that they at any rate considered that the law correctly represented the facts.

Darwin, in the 'Origin' (p. 387, 6th ed.), says:—"So again it has been shown that generally the embryos of the most distinct species belonging to the same class are closely similar, but become, when fully developed, widely dissimilar. A better proof of this latter fact cannot be given than the statement by v. Baer that the embryos of Mammalia, of birds, of lizards, and snakes, probably also of Chelonia, are in their earliest states exceedingly like one another, both as a whole and in the mode of development of their parts; so much so, in fact, that we can often distinguish the embryos only by their size. In my possession are two little embryos in spirit, whose names I have omitted to attach, and at present I am quite unable to say to what class they belong. They may be lizards or small birds, or very young Mammalia, so complete

is the mode of formation of the head and trunk in these animals."

This, I think, shows quite clearly Darwin's view of the matter.

Huxley, in his 'Man's Place in Nature,' says:—"The history of the development of any other Vertebrate animal—lizard, snake, frog, or fish—tells the same story. There is always, to begin with, an egg having the same essential structure as that of the dog; the yolk of that egg undergoes division or segmentation, as it is called, the ultimate products of that segmentation constitute the building materials for the body of the young animal; and this is built up round a primitive groove, in the floor of which a notochord is developed. Furthermore, there is a period in which the young of all these animals resemble one another, not merely in outward form, but in all essentials of structure, so closely, that the differences between them are inconsiderable, while in their subsequent course they diverge more and more widely from one another."

The Significance of Ancestral Rudiments in Embryonic Development.

The existence of a phase at the beginning of life during which a young animal acquires its equipment by a process of growth of the germ, is of course intelligible enough. We see such a phase in the formation of buds, and in the sexual reproduction of both animals and plants. The remarkable point is that while in most cases this embryonic growth is a direct and simple process—e.g. animal and plant buds, embryonic development of plant seeds—in some cases—e.g. most cases of sexual reproduction of animals—it is a circuitous one, and the embryonic phase shows stages of structure which seem to possess a meaning other than that of being merely phases of growth.

As is well known, the explanation which is given of this circuitous course of embryonic development is that we are dealing with a special case of the law of heredity—"each

organism reproducing the variations inherited from all its ancestors at successive stages in its individual ontogeny" ('Comp. Emb.,' vol. i, p. 3).

"These two principles, namely, that slight variations generally appear at a not very early period of life, and are inherited at a corresponding not early period, explain, as I believe, all the above specified leading facts in embryology." (Darwin, 'Origin,' p. 392, ed. vi.)

But this explanation, though good as far as it goes, is not entirely satisfactory, because it fails to explain (without further qualifications) the majority of cases (animal and plant buds, embryonic development of seeds) in which ontogeny presents no ancestral traces; it is at variance with the fact that in many cases variations which affect the adult have affected the whole of embryonic development (see below); and it does not enable us to understand why some organs, e.g. gill slits, have been retained in embryogeny, whereas other organs which have much more recently disappeared, e.g. teeth of birds, fore-limbs of snakes, have been entirely lost. It assumes that the repetition of ancestral characters in embryogeny is the intelligible rule; and that their omission is the exception which requires explanation whenever it occurs. This assumption is not warranted by the fact above indicated that in the vast majority of ontogenies there are no phylogenetic traces, nor by the consideration that a number of important organs, such as teeth and hand-claws in birds, limbs in snakes, gill-clefts in fishes, have recently disappeared without leaving a trace in ontogeny.

In fact the balance of evidence appears to me to point most clearly to the fact that the tendency in embryonic development is to directness and abbreviation and to the omission of ancestral stages of structure, and that variations do not merely affect the not-early period of life where they are of immediate functional importance to the animal, but, on the contrary, that they are inherent in the germ and affect more or less profoundly the whole of development.

I am well aware that in holding this opinion I am running

counter to the great authority of Darwin. In the chapter from which the above quotation was taken he gives many facts and arguments in favour of the view that slight variations generally appear at a not very early period of life, and are inherited at a corresponding not early period. He admits that larger variations—monstrosities—do affect the embryo at a very early period, but he thinks that slight variations do not. Without considering the difficult question as to where the line should be drawn between a slight variation and a monstrosity, I may merely point out that Darwin's evidence is largely based upon the experience of breeders that it is impossible to tell until some time after birth what will be the merits or demerits of their young animals. In mitigation of the force of this fact it must be remembered that a successful breeder is a highly skilled man—that he possesses powers of observation greater than the ordinary—that his success depends upon his ability to see points which escape the eye of other people. If the points for which the mature animal is selected are thus difficult of observation, can we wonder if it is beyond the power of man to see them when the animal is immature, and the relative sizes of the parts of the animal, and its whole appearance, are so different? In support of this way of looking at the matter I would urge that when the variation is large and of a nature to be easily observed, it can—in a great many instances at any rate—be detected all through development.

The evidence is of this kind :—(1) Organs which we know have only recently disappeared are not developed at all in the embryo. For instance, the teeth of birds, the fore-limbs of snakes, reduced toes of bird's foot (and probably of horse's foot), the reduced fingers of a bird's hand. These are instances which readily occur; I have no doubt that many others might be quoted by anyone giving attention to the matter. (2) Organs which have (presumably) recently become reduced or enlarged in the adult, are also reduced or enlarged in the embryo. Many examples of this might be given, and it is a most important point as showing the manner in which variations have

affected the whole of embryonic development. As examples I may mention the small outer toes on the feet of the pig and probably of other Ungulates, the large digit of the ostrich's foot and of the kangaroo's foot, the spiracle of Elasmobranchii,[1] the rudimentary character of the phalanges of the bird's hand. I have no doubt that many other instances will occur to my reader. (3) Organs which have been recently acquired may appear at the very earliest possible stage; e.g. the double hallux present in some breeds of fowls makes its appearance as soon as the other digits; the webbing of the duck's foot is not preceded by a stage in which the digits are separate. In short, the evidence seems to indicate that in a great number of cases adult variations of any part are accompanied by precedent similar alteration of the same part in the embryo. I do not mean to affirm that the alteration of the organ in

[1] The spiracle of Elasmobranchii is a reduced gill-cleft, and in correspondence with its reduction in the adult it is found to be reduced also in all stages of its development from its very first appearance, which takes place after the hyobranchial cleft—not before it, as would be expected from its position as the anterior member of a series (see Self, "Notes on Elasmobranch Development," this Journal, vol. xxxiii, p. 572). It would be excessively interesting in this connection to ascertain whether any trace of the spiracle is present in the embryos of those Elasmobranchs in which it is absent in the adult. In fact, an account of the spiracular cleft throughout the Vertebrata is much needed. Is it present in embryo in Teleosteans and in Lepidosteus? Balfour asserts that it is present in the former ('Comp. Embryology,' vol. ii, p. 77, mem. ed.), but I am unable to find his authority for the statement. He also states that it is present in the embryo Lepidosteus as a double layer of cells without a cavity (Balfour and Parker on 'Anatomy and Development of Lepidosteus,' mem. ed., pl. xxxvii, fig. 43), but, so far as I am aware, his interpretation of this structure has not been confirmed. In Amniota—throughout which the pharyngeal clefts present a very remarkable constancy—the spiracular cleft is as large, if not larger, than the succeeding one, and appears first in development. This is an exceedingly interesting fact, which has not been sufficiently noted. It tends to show that the Amniota have arisen from aquatic forms independently of the terrestrial Amphibia, in which group the spiracular cleft is not formed at all—though a slight rudiment of it does appear for a short period. In fact, we may take it as a fact of systematic value that the spiracular cleft is absent or rudimentary in all Ichthyopsida while it is present in relatively normal development in all Amniota.

the embryonic stage[1] is the same as it is in the adult. It may be altered relatively more or it may be altered relatively less; the point is that it is altered in the same direction as the adult organ. And this is surely what we should expect when we remember that embryonic development is the preparation of the free form in the most perfect state and at the least expense. If this view is correct that variations are present in the embryo—that an organ which is enlarged, diminished, or suppressed in the adult is correspondingly, or nearly so, enlarged, diminished, or suppressed in the embryo,—then I ask, how are we to account for those cases which most undoubtedly occur in which records of previous states of structure are present in the embryonic history, e. g. the pharyngeal slits of Sauropsids, the tubular heart, the vascular arches, the embryonic kidney of the same group, and many such. The point is this: organs which have been recently altered show a similar alteration in the embryo, whereas some organs, like the gill-slits, which must have been altered very far back, do not show a corresponding embryonic alteration, but persist more or less in their old form without discharging the original functions or being of any use to the embryo. In other words, some ancestral organs persist in the embryo in a functionless rudimentary (vestigial) condition and at the same time without any reference to adult structures, while other ancestral organs have disappeared without leaving a trace. The latter arrange-

[1] It appears that in some cases, at least, it is less in the embryo. E. g. sternal ribs of ostrich are generally five in adult, rarely six; in embryo, they appear always to be six. In birds the fibula reaches the tarsus in embryos, but very rarely does so in adults.

A case of this kind which might be investigated is this:—In the golden plover the hallux is entirely absent, whereas in other plovers it is present. Has the golden plover any trace of it in the embryo?

I am aware that it is often held—Darwin held it—that rudimentary organs are, relatively to the adjoining parts, larger in the embryo than in the adult. But unless this fact can be shown to be universal, it has but little value because it applies to many other organs in the embryo which are not rudimentary, e. g. brain, eye, heart, and kidney. This difference in relative size is probably simply owing to the fact that the bulk of the skeletal, muscular, and connective tissues of the embryo is relatively less than in the adult.

ment seems to be the rule, the former the exception. How are we to account for the exception? The key to the position is, in my opinion, to be found by comparing the conditions of larval and embryonic development. In larvæ the organs are functional and the animal is getting its own living during the development, whereas in embryos the development takes place under the protection of egg membranes, the pupal case, or the uterine wall, and the organs are for the most part functionless, special arrangements being made for the supply of nutriment. These two developments have generally not been properly distinguished by naturalists writing on this subject.

In embryos the organs are for the most part functionless and without relation to the maintenance of life; consequently there is nothing to counteract the tendency to the appearance of a variation at all stages in the life of an organ. In larvæ, on the other hand, the organs are functional and the conditions of life may be different from those of the adult. They have to maintain themselves during the various phases of their development; consequently if a variation of an organ at one stage is injurious to the same organ at a previous or subsequent stage, it will be eliminated at the stages at which it is injurious. In this way, as will be readily seen, natural selection will compel the limitation of variations in an organ to particular stages in the development of that organ; the power of natural selection will inevitably prevent a variation useful at one stage from affecting another stage of the same organ in which its presence would be injurious to the larva. Thus there must be in larvæ a tendency to the inheritance of variations at corresponding periods, and to the elimination of them at other periods when they would be harmful to the organism. Thus it must happen that if variations occur which enable the adult to change its condition of life, and if at the same time the old habits of life are retained by the last larval stage, then the old arrangement of organs will be retained by the larva. In this way, as the adult form gradually progresses in evolution, not only one but a whole series of larval stages might become established, each one being based upon some ancestral stage of

structure and retaining some ancestral habit of life. But of course these larval stages are liable to vary and are subject to the natural selection engendered by the struggle for life. So they may themselves become modified and the ancestral habits and structure which they have inherited may also become modified. It thus becomes apparent that larvæ will often retain traces more or less complete of ancestral stages of structure, and that they will do this in virtue of the operation of the force of heredity and of natural selection. And the retention of ancestral features by the larvæ will be the more complete the more completely the ancestral habits of life are retained by them. There is, then, in larvæ a tendency to the inheritance of variations at corresponding periods, and in this respect larvæ differ from embryos.

To sum up, I would maintain that ancestral stages of structure are only retained in so far as they are useful to the free-growing organism, i. e. to the larva in its free development. Or, to put the matter in another and more recondite form, modifications appearing in and affecting the adult structures will similarly affect the same structures all through the development of the offspring unless the old structural arrangements are called into being in the development of the offspring by the application of the old stimulus, viz. the same external conditions of life.

In embryos, on the other hand, the organs are for the most part functionless, and there appears to be no reason for the retention of ancestral conditions of structure. On the contrary, as I have shown above, most organs when modified in the free-living state are similarly modified in the embryo. And, as I have already insisted, this is what we should expect when we remember that embryonic development is the preparation of the free form in the most perfect state and at the least expense. How is it, then, that we do get in embryos in certain cases a most remarkable preservation of ancestral organs and conditions of structure which have been lost in the adult? I think it can be shown that the retention of ancestral organs by the larvæ after they have been lost by the adult is

due to the absorption of a larval or immature free stage into embryonic life.

Let us take an example. Let us try to picture to ourselves the steps by which the tadpole stages of the frog might be lost, so that the adult frog arose direct from the egg. The larval organs of a tadpole cannot disappear one by one independently of one another. If the gill slits disappeared before the heart had become double and the lungs had developed, the tadpole would die of asphyxia. In order to completely obliterate the piscine stage from the tadpole, you require a number of nicely co-ordinated variations affecting different organs in very different ways—all tending to the atrophy of those organs which adapt it to an aquatic life and to the development of the organs required for terrestrial life. Such a combination of suitable variations as is here required—such an inversion of the original evolutionary changes —is very unlikely to occur,[1] especially when the same object can be obtained, namely the obliteration of the piscine phase in the frog's life, by a simple single variation—that is to say, by the mother becoming viviparous and retaining its young within its uterus or oviduct until the piscine stage of development has been passed through; or by the ovarian ovum developing a greater amount of yolk, so that the whole development up to the close of the piscine stage can take place before hatching at the expense of the yolk. That larval stages do disappear and embryonic stages arise in this way is shown by the case of the viviparous salamander (Salamandra atra), in which the gills, &c., are all developed but never used, the animal being born without them. Here, therefore, is an actual case in which the larval phase has disappeared by becoming embryonic and therefore functionless, and therefore largely removed from the direct action of natural selection; once em-

[1] It has suggested to me here that this combination of variations must have taken place in phylogeny, otherwise the terrestrial animal could not have been evolved; why not then in the larva? To this I reply: there is no necessity for the long and laboured changes to be gone over again in inverted order in the case of the tadpole, because the object can be obtained by the simple inclusion of the tadpole stage within the embryonic period.

bryonic only, the conditions of its existence are totally altered. Its disappearance is no longer a matter of importance to the organism, because the embryo being protected from the struggle for existence the presence of rudimentary functionless organs is unimportant to it. They therefore persist, and it is this persistence which has given rise to von Baer's law. But von Baer's law is imperfect, because it omits to take cognisance of the fact that embryonic features are no more constant than are the adult characters; that indeed they vary with the adult characters, so that no adult character is changed without some precedent alteration of all the previous embryonic phases. The embryonic life is a connected whole, and it is impossible that an isolated alteration of one particular stage can have taken place. All variations must run through the whole development; they may come out strongly at one particular stage, but they must have been led up to and followed by variations in all other stages.

Embryonic variations are not for the most part acted upon by natural selection, because they concern rudimentary organs only; but when free life is reached, and the organs become functional, the same variations continued (for continue they must) are put to the test, and the organism stands or falls by them. The constancy of development in the same species proves this point; for if the embryonic stage could vary without the free stages being at all affected, then, as natural selection does not act upon rudimentary embryonic organs, the embryonic organs would run riot, and we should expect to find the greatest diversity in embryonic development of the same species, and this we do not find; and this applies not only to organs which persist into the adult, but also to organs which disappear before the adult stage is reached. These purely embryonic structures must have some nexus with structures which succeed them in development, and a variation in them must be accompanied by variations in these later appearing persistent organs. In fact, it seems to me most important to remember that the various stages in the development of an animal are just as much correlated as are the different organs

of the adult animal with one another. I repeat, the constancy of development in the same species proves this point, as do the small but constant differences between the embryonic phases of slightly different but distinct species.

Granting that embryonic rudiments do vary, of which I do not think there can be any doubt, then it would appear that the variations must be selected, not with regard to their intrinsic[1] merits at the moment as is the case with variations in functional organs, but with regard to the effect of their descendent or correlated variations in the adult. So it comes about that the embryonic rudiments in one group of animals, though resembling generally those of another group of the same class or phylum (just as the functional adult organs resemble one another generally), yet differ from them in minor points, so that the group has its own individual character with regard to that particular rudimentary organ, just as it has its own individual character with regard to any adult functional organ.

The conclusion here reached is that, whereas larval development must retain traces (it may be very faint) of ancestral stages of structure because they are built out of ancestral stages, embryonic development need not necessarily do so, and very often does not; that embryonic development, in so far as it is a record at all, is a record of structural features of previous larval stages. Characters which disappear during free life disappear also in the embryo, but characters which though lost by the adult are retained in the larva may ultimately be absorbed into the embryonic phase and leave their traces in embryonic development.

[Throughout the above discussion I have, to avoid complication, treated all embryonic organs to be functionless; but it

[1] By intrinsic merits at the moment, I mean the effect on the organism as a whole at any particular moment. A variation in a rudimentary functionless organ of an embryo can have no effect upon the welfare of the embryo (excluding secondary effects—if any—of interfering with functional organs, e. g. blood-vessels); its utility can only be judged when the free state is reached.

must not be forgotton that some of them are functional and that these resemble organs of larvæ in retaining ancestral features, e. g. the ductus arteriosus, &c.]

To put the matter in another and more general way, the only functionless ancestral structures which are preserved in development are those which at some time or another have been of use to the organism during its development after they have ceased to be so in the adult. In this way I should be inclined to explain the hair of the human fœtus and the teeth of the fœtal whale—that is to say, I should be inclined to suppose that the possession of the lanugo is due to the fact that there was a time in the evolution of man when the babe required this protection against the cold after the necessity for it had disappeared in the adult, and that the young whale in the days when whalebone was first acquired still retained the ancestral habits which required teeth. It is, however, possible that these and other similar cases of the retention of rudimentary organs in late embryonic life have another explanation, and it becomes necessary to collect and examine as many cases as possible of the undoubted retention, as embryonic rudiments, of organs which we have reason to know have recently disappeared from the adult stage.

The retention of such organs in the embryo may, as I have hinted, be due to the fact that they have been retained functionally by the young animal after they have been lost by the adult; but another explanation is possible, which is that organs which are becoming functionless, and disappearing at all stages, may in some cases disappear unevenly; that is to say, they may remain at one stage after they have totally disappeared at another. In this manner we might get an organ which had become quite functionless and had quite disappeared in the free stage, still persisting, though with a much reduced development, in the embryo. It is possible that the lanugo and the teeth of fœtal whales may be explicable in this manner. But that such a retention of organs in the embryo is not an important or permanent one is shown by the fact of their comparative scarcity in embryonic histories. This is a

most important subject, and I propose in a future paper to collect and examine as many cases as I can find of the retention in the embryo of organs which have lately disappeared in the adult.

There is another aspect of the same question which is suggested by the above considerations, viz. if an organ can disappear unevenly there is no reason in the nature of things, so far as I can see, why it should not disappear in its devoloping embryonic stages before it does so in the adult, so that there would still be found in the adult a persistent useless rudiment of it after all trace had gone in the embryo. And we may even go further than this, and maintain that if organs can disappear unevenly it is conceivable that traces of an ancient organ might appear and disappear more than once in the course of development. Of the last-suggested phenomenon I know of more than one instance, but I know of no instance of an organ disappearing in its embryonic stages while still persisting as a rudiment in the adult. As an example of the repeated appearance and disappearance of a rudimentary organ in embryonic development I may mention the neurenteric canal of certain species of birds as described by Gasser,[1] and quoted by Balfour in the 'Comparative Embryology' (vol. ii, p. 162, mem. ed.). The anterior neuropore of Ascidians, which appears twice in the development, is another example of the same phenomenon. Although I know of no instance of an organ disappearing in the embryo before it totally disappears in the adult, I do know of instances of rudimentary embryonic organs which have disappeared in their earlier stages while still present at a later stage, e.g. the muscle-plate cœlom of Aves, the primitive streak of Amniote blastoderms, and the neurenteric canal of Aves; and I have no doubt that many instances of this might be collected.

From the application of the principles set forth in the preceding pages it becomes apparent to us why it is that in the

[1] Gasser, "Der Primitivstreifen bei Vogelembryonen," 'Schriften d. Gesell. zur Beförd. d. gesammten naturwiss.,' zu Marburg, vol. ii, sup. 1, 1879.

higher animals it is the early stages of development which have the greatest interest for us, the later stage having been added at a time when, as now, the immature stages of free life were but little marked, and consequently there was but little chance of the incorporation of any ancestral features in the embryonic development. It also helps us, I think, to understand why the most interesting of the ancestral embryonic features were related to the passage from the aquatic to the terrestrial condition, because when this took place in phylogeny there must have been a most pronounced aquatic larval stage, such as we find to-day in Amphibia.

Appendix.

Mr. J. J. Lister has pointed out to me as confirmatory of the views set forth in the preceding pages that there is at least one exception to the rule that animals produced by budding show no ancestral rudiments in their development, viz. the sexually mature medusoid spore-sacs. These organisms present in their development traces, as is well known, of many organs which they must formerly have possessed in a functional condition, e. g. the umbrella cavity, the marginal tentacles, the circular canal, &c.; but, as Mr. Lister points out, these sporesacs differ from other buds in this important fact that they have most undoubtedly had quite recently a free life during the maturation of the generative products; and it may be that it is the impress of this ancestral free life which has given rise to the ancestral features in the development.

A Contribution to our Knowledge of the Annelida.

On some Points in the Structure of Euphrosyne.

On Certain Young Stages of Magelona and on Claparède's unknown Larval Spio.

By

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With Plates 6—8.

On some Points in the Structure of Euphrosyne.

In the circumstances under which the present paper is contributed, it is perhaps fitting that a form should be selected (viz. Euphrosyne) which first came under my notice by the kindness of Professor Ray Lankester, who sent preparations procured in Herm in 1865. When an opportunity occurred a few years later (1868) of becoming familiar with living examples on the same ground, unfortunately time did not permit a detailed investigation of internal structure, and accordingly I have had to content myself with the examination of rather imperfect spirit-specimens.

While the structure of the genus Spinther, Johnston, has been more or less fully elucidated by the labours of R. von Drasch ('Anatomie von Spinther miniaceus,' Grube, 1885), and especially by those of Ludwig von Graff ('Die Annelidengattung Spinther,' 1887), the present genus, so far as I can ascertain, has received attention only from Schmarda[1] and E. Ehlers;[2] but at the date of their treatises the modern

[1] 'Wirbellosen Thiere,' 1, ii, p. 136, pl. 33, figs. 264, 287.

[2] 'Die Borstenwürme,' i, p. 67, Taf. i and Taf. ii, 1864.

methods of microscopic investigation had not been introduced. The sections were made from examples of Euphrosyne foliosa, Aud. and Ed., and a few from E. cirrata, Sars, a northern species, kindly sent by Canon Norman; and I have to thank Mr. C. H. Williamson, M.A., B.Sc., for preparing and mounting the slides; and also for aid in this respect from Mr. A. T. Masterman, B.A. (Cantab.).

Body-wall.—The cuticle is of considerable thickness, and in the dorsal region and some other parts has externally in the preparations a striated granular coat, which may be connected with the presence of cilia. It is, on the whole, somewhat thicker than in Spinther. The hypoderm beneath has the usual structure, and is very thin in the mid-dorsal line, but increases laterally, and again ventrally. The inner edge is sharply defined, so as to separate the circular muscular coat distinctly, but a definite basement-layer does not appear to be formed. Proportionately this layer is somewhat less developed than in Spinther. The circular muscular coat lies immediately beneath the hypoderm in the form of a continuous sheath, though in the dorso-lateral regions it is modified; the main mass, however, bounding the perivisceral chamber and forming a thick ventral layer, pierced here and there by the fibres of the vertical and oblique muscles. In the lateral regions a radiate arrangement of powerful muscles takes place in connection with the bristles; indeed, a double radiate arrangement is present in many sections where the upper and lower series of bristles come in the way of the knife.

The longitudinal muscular layer forms dorsally a series of fine fasciculi beneath the circular, and it follows the latter in its course outside the perivisceral chamber, attaining its maximum thickness after the splitting of the circular coat. Ventrally the powerful longitudinal muscles are grouped in large fasciculi separated by the vertical or oblique strands which pass to the circular layer. The fibres from the oblique muscles decussate beneath the nerve-cords, many mingling with the circular (Pl. 7, fig. 4). The latter feature is much less evident in

Spinther; indeed, none of von Graff's figures indicate it, and no allusion thereto occurs in his description.

Caruncle.—In horizontal section this highly sensitive tongue-shaped organ presents externally a thin layer of cuticle, the greater part of the area internally being formed of hypodermic cells and granules. Posteriorly, in the middle line, however, is a double fibrous band, with at intervals various lateral fibres, which extend not only into the lateral regions but also into the narrow spaces between the bands. About the middle of the organ one band becomes prominent and its fibres spread more and more outward on each side until the eyes are reached. These fibres are probably contractile. In such a section as in Pl. 1, fig. 1, the pennate arrangement of the median fibres is conspicuous, and they merge laterally into the hypoderm. Moreover, in this section the complex muscular fibres which intercross at the margins, and which apparently are connected with the flattening of the organ, and other changes in its outline are clearly shown.

In vertical section (Pl. 6, fig. 2) the caruncle has a more or less radiate appearance, due to the fibres which diverge from the inferior area into the surrounding cellular stroma of the hypoderm. The area referred to increases in size from behind forward, and in many views has a definite boundary or arch of decussating fibres superiorly. It (that is, the space below the arch) is occupied by a series of vertical fibres which radiate superiorly into the substance of the caruncle, and cause the somewhat arborescent appearance of the organ in section. While, therefore, the lower fibres in the area just mentioned are vertical, the upper are less definitely so. On the other hand, the fibres are almost wholly vertical in the small or undeveloped condition of the area posteriorly, since they pass straight upward to diverge into the tissue of the caruncle. Below the latter the muscular fibres form a powerful band, which by-and-by are interlaced with longitudinal fibres in conspicuous meshes (Pl. 6, figs. 2 and 3). The origin of these fibres would appear to be the raphe above the folds of the mouth. The area diminishes anteriorly, and seems to be occu-

pied chiefly by the cut ends of longitudinal fibres, while the fibres bounding it form a dense fillet. In vertical section (Pl. 6, fig. 2) the radiate arrangement of the fibres from the arch or fillet is well shown, and they constitute a series of loops or meshes between the arch and the hypoderm. The area itself is occupied by vertical and oblique fibres which come from the dorsum in powerful bands, and which have longitudinal fibres here and there in their meshes.

In Euphrosyne cirrata, Sars, from Norway, a conspicuous strand of fibres passes from the nerve-masses (now at the ventral surface) to the caruncle (Pl. 7, fig. 1), while other fibres converge from the neighbouring region to the same organ. Immediately over the cephalic ganglia in this species the area presents only fine fibres at the sides of the median space, and a large amount of opaque granular matter occurs at the sides of the organ, partly mixed with the hypodermic tissue and partly in a special capsule at each side, and apparently represents a pair of glandular organs. The granular substance has not been stained. Posteriorly (before the termination of the cephalic ganglia) well-marked median and radiate fibres appear in the caruncle; then bands pass from the lateral regions both into the latter directly and into the median longitudinal band in front of the descending nerve-mass. A very complete raphe is formed, and the distribution of the fibres is so arranged that the organ and the region below it can be directly pulled. The caruncle can thus be elevated or depressed. After the nerve-mass has become wholly ventral, strong muscular fasciculi pass from the ventral wall to the base of the caruncle, and spread out on each side of it; then the band is chiefly median and attached to the base and to the small knob representing the organ posteriorly. The caruncle in this species differs considerably in external form from that of Euphrosyne foliosa, being more or less elongate and free, and the tentacle is likewise filiform. The latter merges into the base of the former anteriorly (Pl. 7, fig. 1).

In Euphrosyne foliosa a pair of closely approximated eyes lie at the anterior part of the caruncle (Pl. 6, fig. 3, *ocd.*),

and another even more closely approximated pair on the ventral surface of the snout in front of the two prominent pads of the mouth (ibid., *ocv.*), and thus separated from the dorsal pair by a considerable interval. Functionally thus the one pair serve as organs of vision dorsally, the other for use ventrally. The eyes have a distinct capsule with a broad margin of pale columnar cells, within which is the dense black pigment.

In Spinther the tentacle is apparently homologous with the caruncle in the present genus. It lies over the cephalic nerve-mass, is supplied with two large nerves, four eyes, and considerably developed hypoderm, but the latter and the muscular strands are much more largely developed in Euphrosyne, and the organ is more complex. Vertical muscles pass from the nerve-cords inferiorly in Spinther, and other muscles from the lateral regions outside the pharynx, but they are less developed than in Euphrosyne. The situation of the eyes in Spinther, however, diverges, since both pairs are dorsal in position, being located at the anterior and posterior margins of the tentacle. The figures of Drasche[1] and von Graff,[2] as well as my own sections of Spinther miniaceus, Grube,[3] show that the minute structure of the eyes is the same in both genera.

In Euphrosyne cirrata the dorsal eyes lie on each side of the anterior region formed by the fusion of the tentacle with the caruncle. They have a somewhat radiate arrangement of the clear vesicles with a dense ring of pigment, and lie in the hypoderm—with the cuticle externally. The ventral pair are more widely separated than the dorsal, but have the same structure and relations to the hypoderm and cuticle.

Branchiæ.—Externally are the cuticle and its cilia—with the thick hypodermic layer beneath—both layers being continuous with those of the body-wall. Moreover, vertical bands of muscular fibres pass through the circular and other layers to the bases of the branchial stems, enter the latter, and form

[1] 'Anat. von S. miniaceus, Grube,' Wien, 1885, p. 10, Taf. ii.

[2] Op. cit.

[3] I am indebted to Professor L. von Graff for various examples of this species.

the central longitudinal fibres. The shortening and elongation of the organs is thus explained. In vertical sections (Pl. 6, fig. 6) many transverse fibres occur between the longitudinal, often crossing at right angles to the latter. Though in such sections the fibres appear to be characteristically transverse, yet in transverse sections of the basal region (Pl. 6, fig. 4) they present a radiate aspect, passing in front and behind the lumen of the blood-vessel on each side.

These radiate fibres will readily alter the calibre of the stems, expansion again occurring probably by the elongation of the longitudinal fibres and the distension caused by the blood. The inner margin of each blood-vessel is well defined, apparently by a special coat, while the coagulated blood occupies the central space. Externally the connective tissue and other fibres of the branchial stem are closely united with the vessel, so that no separation other than what has been mentioned exists. In longitudinal sections in which the two vessels are slit symmetrically, the lateral regions are occupied by the latter (vessels), the median by transverse and longitudinal fibres. The constricted region below the tip is circular in transverse section, with the hypodermic cells radially arranged around a central point, for the blood-vessels are now absent (reaching only to the commencement of this narrow region, as in Pl. 6, fig. 5), and the fibres pass into the centre of the dilated terminal region almost to the tip. In the terminal part the large cells of the hypoderm (which give it a vesicular appearance) are also somewhat radially arranged—often sloping from the central axis outward and upward in vertical section, or placed regularly around the central axis in horizontal sections. The tissue in these dilated regions is therefore much more lax than in the constricted region beneath, as Ehlers observed. He also describes a slender, circular muscular coat externally (that is, within the hypoderm), but the preparations did not satisfy me on this point, though in Euphrosyne cirrata certain transverse wrinkles were seen at the base in longitudinal sections. Besides, the arrangement of the radial fibres would indicate that the functions of such a coat are fulfilled by

other means. Shortening and elongation of the organs may occur without the presence of circular fibres.

The absence of specially developed branchiæ in Spinther is interesting, but the perivisceral fluid as well as the blood-vessels are in this form nearer the surface, and the great hypodermic membranous flaps on the dorsum may in some respects also subserve this function. The intimate connection of the lateral lamellæ with the bristles may also prove of importance, since the muscles of the bristles must cause extension of the membranous lamellæ.

Dorsal Cirri.—Externally is the somewhat granular layer covering the cuticle, a condition probably due to the cilia, which Ehlers describes as being largely developed. A thick layer of hypoderm occurs beneath, with large cells here and there. Both layers are continuous with those on the body. The hypoderm at the extremity of the cirrus is finely granular and longitudinally streaked, and the cuticle of this region is very thin. Vertical fibres from the body pass upward into the base of the cirrus and thence to the tip of the organ. Only a few circular muscular fibres were observed at the base of the cirrus (under the hypoderm), the elasticity of the cuticle probably sufficing to restore the shape of the organ on relaxation of the longitudinal fibres. These organs are not represented in Spinther.

Alimentary Canal.—On viewing the alimentary canal from the dorsum in a spirit preparation of Euphrosyne foliosa (Pl. 7, fig. 2) the proboscidian region (Schlundkopf, Schmarda) has a somewhat ovoid outline, and is slightly narrower in front than behind. It is divisible into two regions, for anteriorly a glistening whitish layer (*a*) envelops like a sheath rather more than the anterior third, splitting in the middle line and curving outward on each side, so that its outline resembles that of a bivalve shell. Inferiorly this sheath preserves an unbroken transverse border posteriorly. The enlarged posterior region is free beneath, but dorsally terminates in a canal (*b*) connecting it with the intestine at *d*. The outline given in Pl. 7 differs considerably from the organ in

Schmarda's Euphrosyne polybranchia, in which the region presents a series of frills posteriorly and only two papillæ or bosses in front.

Behind and above the rounded muscular mass of the protrusible pharynx is a chamber with thinner walls, and having laterally a series of well-marked rugæ (*e*). This chamber may represent the stomach, as Ehlers states, and it is connected with the intestine at *d* as above mentioned.

The mouth (Pl. 6, figs. 3 and 7, *w*) opens on the ventral surface between the third and the fifth segments, as Ehlers describes in E. racemosa, and the walls of the buccal chamber are thrown into many complex folds (*wf.*) which externally have a cuticular coat. These folds are continuous with the walls of the proboscis. In transverse section the latter presents in front a closely interwoven series of muscular fibres chiefly circular and oblique, though vertical also occur. Moreover, large blood-vessels are visible ventrally at the sides. The eversible portion of the organ has both inner and outer surfaces coated with the cuticle (which is stained), and the finely granular and streaked hypoderm beneath is well marked, besides certain muscular fibres passing into the bases of the papillæ. In all probability it is the latter processes which Schmarda describes as horny teeth in Euphrosyne polybranchia.

The buccal chamber gradually enlarges into a flattened canal above (i. e. dorsal of) the posterior portion of the great muscular "stem" of the proboscis. The latter (stem) is composed of a complex series of fibres, the ventral being chiefly arranged in parallel and vertical bundles, and bounded by a definite investment, a few longitudinal fibres being clasped in the interstices. Moreover, this region is cut off by a thin cuticular septum from the part above. Then the median region is occupied by a dense mass of glandular tissue (Pl. 6, fig. 7, *gl.*), the glands being large and granular and extending to the hypodermic coat which, with the cuticle, bounds the chamber now present in the organ at this part. These glands apparently perform an important part in the functions of the region. The

upper arch again has transverse muscular fibres close to the hypodermic border. A powerful muscular mass exists above, ending in the thin hypodermic and dense cuticular layers bounding the floor of the upper canal (Pl. 7, fig. 3). The opposite or upper face of the canal has a very thin cuticular coat and a thick glandular (hypodermic) layer. Folds or ridges next appear at the sides (Pl. 6, fig. 7, *e*) where the dorsal arch joins the muscular stem of the proboscis, and they pass dorsalwards on this arch in the form of an extended ridge on each side in transverse section, the surface being hypodermic, while beneath is areolated glandular tissue. Proceeding backward these lateral ridges increase in size, and instead of an even surface show prominent ridges, while by-and-by a belt of this folded tissue passes entirely across the upper chamber. Inferiorly the stem of the proboscis now presents a somewhat regularly interwoven field of cross-fibres like meshwork, bounded ventrally by a rim of longitudinal fibres, the upper edge being defined by a cuticular investment. Beyond the longitudinal belt at the ventral border of the decussating fibres is a broad belt of vertical fibres.

The chamber soon shows a regular series of transverse ridges of hypodermic glandular tissue, and then terminates in the intestine. Externally is a layer of longitudinal fibres, internally a coat of circular fibres, and the glandular lining has cilia on its surface.

In longitudinal section (Pl. 6, fig. 7) the mouth has various prominent folds of the lining membrane in front, but the anterior region of the proboscis in this species did not present the regular series of papillæ indicated in the figure of Professor Ehlers. The main channel passes dorsally, and reaches the thin-walled chamber marked *bs.* in fig. 7, Pl. 6. The dorsal wall agrees with that shown in Pl. 7, fig. 3, though the cuticular layer is less marked, and extends to the opening into the intestine. In this chamber the ventral surface is formed by a portion with bold ridges (*br.*, fig. 7, Pl. 6, where a part only is shown, as the section is not median). In the ordinary or retracted condition of the parts the food would thus be acted

on by the area with the ridges and the powerful muscles beneath, so that—between muscles and glands—a considerable alteration probably ensues. There are grounds, therefore, for thinking that this chamber represents the stomach, since its posterior end leads by a short canal directly into the intestine.

The intestine follows the short canal just mentioned, and consists of a wide passage, usually thrown in the preparations into deep folds—with a few shallow diverticula of its walls; but, so far as spirit-preparations can be relied on, the diverticula do not attain the dimensions shown by Ehlers in his E. racemosa.[1] The canal has a thick wall of densely granular glandular tissue, papillose internally, and of circular fibres externally. It continues backward and terminates posteriorly in the vent, which is situated between two prominent lips just in front of the caudal papillæ. A differentiation of the gut occurs at the rectum, so distinct that in transverse sections it appears at first sight that an independent channel exists posteriorly. The continuity of the mucous membrane is, however, easily made out. In this region, which is somewhat triangular in transverse section, the thin membranous investment has beneath it a layer of longitudinal fibres, and the adjacent granular cells more resemble those of the hypoderm than the homologous cells of the intestine. Portions of food and sand are occasionally observed in the centre of this portion of the canal.

The food consists in some of a soft mass in which cells, spicules of sponges, chitinous fragments, and other débris are present; while in others little else than sponge-spicules can be seen. Posteriorly the cylindrical fæcal mass usually occupies the centre of the gut. In Schmarda's species calcareous fragments, bristles of Annelids, and sponge-spicules were found. It may readily be concluded, therefore, that it is difficult to secure either perfection or continuity in transverse sections of the body.

The digestive system of Spinther differs from the foregoing in regard to the much more largely developed lateral cæca of the gut, and the less massively muscular proboscis. The

[1] Op. cit., Taf. ii, fig. 1.

presence of an extensive dorsal blind-gut is another important divergence. Both, however, feed for the most part on the same substances.

Nervous System.—The central mass of the nervous system lies immediately under the caruncle, and consists dorsally chiefly of nerve-cells, ventrally of fibres (Pl. 6, figs. 3 and 8, *cg.*).

The position of the eyes (Pl. 6, fig. 3, *ocd.* and *ocv.*) in Euphrosyne diverges from that in Spinther, for in the latter the four eyes are confined to the dorsum, whereas in the former two are dorsal and two anterior and ventral.

The subœsophageal ganglia form a single mass behind the mouth, with a fibrous central region and two lateral cellular masses as in E. cirrata.

The ventral nerve-cords (which Ehlers states are non-gangliated) lie on each side of the median line enveloped in their sheath, and partly separated superiorly by a fascicle of longitudinal muscular fibres (Pl. 7, fig. 4, *nc.*). The oblique muscles pass down by their external borders to decussate inferiorly. With the exception of the capsule of connective tissue, the cords in section present a granular surface from the cut extremities of the fibres. Beneath the fascicle of longitudinal fibres is a curved strand of transverse fibres (Pl. 7, fig. 4, *cm.*), which forms a commissure between the cords. It is concave from above downwards. In many sections a strand of fibres closes in the space for the longitudinal muscular fibres superiorly. External to the cords are flattened bands of muscular fibres, the decussating fibres of the oblique muscles, and the circular coat with the cutaneous tissues (Pl. 7, fig. 4).

In comparing these cords with those of Euphrosyne capensis, the same fascicle of longitudinal muscular fibres and the firm investment superiorly are characteristic. In Euphrosyne borealis the muscular parts are specially massive. In E. cirrata, again, the nerve-cords, which lie close to the hypoderm, are flattened in section and much more widely separated. A transverse commissure, however, is present.

In Spinther ganglionic enlargements and transverse commissures similarly placed are shown by von Graff. He also describes optic, pharyngeal, œsophageal, and other nerves from the cephalic ganglia.

Circulatory System.—Schmarda was of opinion that in Euphrosyne polybranchia the circulation agreed with the general type of the Annelids. In the midventral line a large vessel occurs, with two smaller lateral trunks which supply the ovaries. The unpaired vessel gives many branches to the alimentary canal. On the dorsum of the alimentary canal are two vessels, from each of which large branches go to the branchiæ. He finds that the vessels have two coats, an outer longitudinal and an inner circular (his transverse); while the blood is red, and shows corpuscles $\frac{1}{200}$ mm. in size. Ehlers adds nothing to this description except to observe that the blood in Euphrosyne racemosa is colourless.

In E. foliosa the ventral vessels are distended by the yellowish and minutely granular blood (in the preparations), and various branches are observed amongst the reproductive elements, but the sections are less satisfactory as regards the dorsal vessels. All that can be said is that a dorsal trunk was seen in certain sections over the alimentary canal, and most frequently in a state of contraction. The inner coat of the larger vessels appears to be a homogeneous elastic one, no circular striæ having been observed, though such may be present in other forms. The outer coat certainly has longitudinal fibres.

At the anterior part of the intestine the sections[1] of four or five trunks are seen in the mid-dorsal line close to the gut or amongst the reproductive elements. All these are empty, the collapsed vessel having a dotted or cellular appearance, and thus different from those distended with blood in the other parts of the reproductive masses. Proceeding forward so as to bring the duodenal channel with its dense walls and inner surface covered with cilia into view, a grouping of these

[1] Which, unfortunately, are less complete than I could have wished, and no additional examples could be procured.

vessels above the latter channel (which lies over the intestine) takes place, so that a large mass, composed apparently of thick striated walls round a central lumen, is soon formed. It is difficult to say what this is, though it possibly may be a specially contractile region of the vessel. It is shown in its fully-developed condition in Pl. 7, fig. 5, *v. g.* It then splits into two trunks which gradually separate from each other as we proceed forward, but they always preserve a dorsal position to the duodenal gut, stomach, and proboscis. They diminish in size as they go forward, but they retain the same structure and contractility. Their mode of termination could not be ascertained.

The structure and arrangement of these parts would point to their connection with the vascular system, but as no vessel contains blood, and as their structure differs from the distended trunks, some doubt exists. Their highly contractile condition may be associated with the functions of the proboscis, which, as formerly shown, has large blood-vessels inferiorly.

Segmental Organs (Nephridia).—Schmarda does not refer to these organs, but Ehlers describes them in his form as reaching to the twentieth segment. They lie under the dorsal wall of the body, and have their external openings in the median line between the branchiæ. Each is in the form of an elongated bifid tube, extending over two or three segments. The two inner openings are trumpet-shaped, with orange pigment and internal cilia. The only structures observed in the sections of E. foliosa are the bifid vessels passing over the proboscidian region from the single dorsal tube as described above, and such would appear to pertain to another system.

Generative Elements.—Schmarda describes the ovaries as funnels or tubes with a blood-vessel in the middle. These tubes end in an oviduct which opens near the vent or near the inner branchiæ. The specimens examined by Ehlers had no generative elements. These elements in E. foliosa occur in the perivisceral space around the alimentary canal, and at the bases of the feet (Pl. 6, fig. 1, *ov.*, and Pl. 7, figs. 5 and 6, *g. p.*). In the male the dense masses of sperm-cells are often arranged

round the blood-vessels, and with the cells somewhat regularly placed in rows, so as to form long loops, concentric or slightly radiate areas. The linear arrangement of these cells, indeed, is characteristic. The same regions are occupied by the large eggs in the female. The sexual elements were best developed in those obtained in July and August, both in Britain and in Norway, and they probably escape dorsally by the nephridia. Many ova occur amongst the branchiæ and bristles of the dorsum. In regard to the escape of these elements, the most likely channels appeared to be those that passed to the skin near the bristle-bundles.

The ova in Spinther are proportionally as large as in Euphrosyne, but no nephridia have been observed, though it is possible they may yet be found.

On Certain Young Stages of Magelona.

The occurrence of several stages of the young of Magelona in the bottom trawl-like tow-net in St. Andrew's Bay gives an opportunity for taking a brief survey of our knowledge of the subject.

Claparède, in 1863,[1] described some young stages of this species which he had procured at St. Vaast la Hougue in the summer of 1861. His youngest form was about 1 mm. in length, and cylindrical. The anterior end formed a wide funnel, and thus differed from any larvæ hitherto found at St. Andrews. The border of the funnel was beset with cilia, and cilia occurred behind it. Four reddish eyes occurred transversely on the dorsum of the head. Between the broad cephalic region and the first body-segment is an expanded region bearing a tuft of long cilia. There are from fifteen to twenty body-segments—which are widest anteriorly. From the projecting process of the first body-segment proceeds the tuft of long smooth bristles, which are almost as long as the body. The following segments had touches of brownish pigment, a pair of small hook-pads, and short bristles. Each

[1] 'Beobachtungen üb. Anat. u. Entwicklungs. Wirb. Th.,' p. 74, Taf. x, figs. 9—14, and Taf. xi, figs. 1, 2.

segment had a ventral band of cilia, whereas none occurred on the dorsum. The terminal segment had a ring of long cilia. The alimentary canal was roseate. This larva is distinguished, he says, from a Leucodore larva by the dilated anterior end, by the brownish pigment-touches, the smooth bristles, by the ventral cilia on all the segments, and by their absence on the dorsal surface.

It exhibits by-and-by a modification of the head, which becomes elongate heart-shaped, and by the development of lateral papillæ from which the tentacles grow behind the eyes. The provisional swimming apparatus, viz. the bands on the head, the lateral tufts, the ventral bands, and the anal ring are all increased.

When it reaches the length of about 2 mm. it approaches a Spio larva, and swims freely in the water by a rapid wriggling of the body. The heart-shaped snout is narrowed in front, concave below, and convex above. The four reddish eyes are larger, and the middle pair placed in advance. The first body-segment overlaps the head, and from its sides spring the short tentacles, which are borne like a pair of horns, the inner side of each being marked by brownish parallel striæ, and the slender papillæ are 0·017 mm. long. The tentacle has a central blood-vessel which ends blindly, and its blood contains corpuscles. The first segment bears the huge bristles, while the last is elongated, cylindrical, and is devoid of bristles. The rows of hooks occur from the ninth segment, some of them in sacs. They are more numerous posteriorly (to the number of fifteen). The posterior ènd is pointed and bears small, colourless, pyriform (birnformige) papillæ. The digestive canal begins with an oval mouth and a muscular proboscis, which has a pair of opaque (brownish) glands at its posterior end. The canal, which is constricted in front, dilates at this point. The colour of the larva is delicate brownish, with parallel bands of the same hue on the tentacles; longitudinal and transverse brownish touches on the snout. The translucent anterior region and the three following segments bear similar touches. The middle fifteen segments of the body have

brownish pigment-rings. The following segments have lateral touches of the same colour, which posteriorly almost assume the form of rings. The tip of the tail is brownish, and the same tint occurs anteriorly at the lips of the proboscis.

His next stage presents elongated tentacles with long papillæ and coiled like ram's horns, yet the snout is even shorter than in the foregoing stages, so that a certain amount of variation exists. The length is 8 mm., and it swims like an eel. Claparède compares the elongated papillæ with the peculiar "stabchen" on the tentacles of Spio as described by Strethill Wright, but the differences are considerable. The first body-segment bears the long bristles. From the second to the eighth segment the lateral bristles have disappeared. From the ninth to the fifteenth long provisional bristles as well as hooks with an elongated shaft are present. The brownish glands behind the proboscis are larger. The blood has a bluish appearance. The end-segment is hoof-like and somewhat resembles that of Leucodore, and it has small coloured warts.

He concludes by mentioning that further stages of Magelona were not got in his nets, and that they probably took to the bottom to burrow in the sand at the extreme margin of low water. He was inclined to relegate the larva to the Spionidæ.

On the present occasion only the more advanced Spio-like forms, approaching Claparède's two last stages, figured in his pl. x, figs. 10 and 12, will be dealt with. The first was obtained on the 28th May, and had about twenty-five segments exclusive of the head and tail. The animal (Pl. 8, fig. 1) is nearly translucent, faint touches of white pigment appearing on the sides of the proboscis posteriorly, at the commencement of the narrow part of the gut, and at the base of the tentacles. An opaque white mass (the contents) also marks the centre of the gut towards the tip of the tail. Lateral opaque white specks in groups further indicate the segments in the anterior (dilated) region of the body. The latter consists of nine segments, the tenth being opposite the whitish opacity (*a*, Pl. 8, fig. 1) marking the commencement of the constricted portion

of the gut. Besides the anterior long bristles, there are several pairs on the sides posteriorly, as shown by Claparède, who figures four pairs in Magelona (ibid., Taf. x, fig. 12). In a coloured drawing of one at this stage by Mr. J. Pentland Smith, M.A., B.Sc., about seven pairs are present. The tentacles are longer than the body, and contain only a single vessel, as in Claparède's stage of Magelona of 2 mm., and no circulation is yet visible, though a few stationary corpuscles are observed on the wall of the vessel. In this condition the Annelid stretches itself freely, with the tentacles widely expanded, and apparently draws in water by the mouth at intervals, to judge from the movements of the gullet. When irritated it coils its tentacles like springs, and wriggles rapidly through the water, as noticed by Claparède in Magelona. Only slender spine-like papillæ occur on these elongated organs, as in Spio, to which the young form has close affinities. No forward growth of the snout has yet taken place, and therefore this example would appear to belong to another form or to be less developed than Claparède's fig. 12. Moreover, the eyes are black, not red, and much smaller than he shows. The pigment of the body further is white, not brownish, such, perhaps, being due to variation. As in other species, such forms do not follow the younger in regular succession as regards date, for the spawning period is evidently prolonged. Thus, for instance, the foregoing example was much larger than some examples of Magelona procured at the same time, or even than others found in the middle of June. Moreover, the shedding of the long larval bristles takes place at different periods in specimens of the same or nearly the same age. They are absent, for instance, in the example figured in Pl. 8, fig. 2, though in other respects it agrees in structure with the foregoing.

On the 17th of October (similar forms, however, having been seen earlier) a more advanced specimen of Magelona than described by Claparède was obtained in the bottom trawl-like tow-net (Pl. 8, fig. 3). The basal part of the tentacles is now furnished with larger papillæ, while the slender processes

formerly mentioned still exist on the terminal region, as, indeed, was observed in some examples in May. The eyes corresponded with those already figured in the Spio-like larvæ (figs. 1 and 2), and are still much less than in Claparède's representations. The snout now forms a flattened spathulate process of considerable dimensions, though it is less in proportion than in the adult.[1] Moreover, no blood yet enters this region (snout), though the circulation in the tentacles is complete. The latter organs can be fixed to the glass vessel by the papillæ, which thus have adhesive properties. Each of the nine anterior segments is furnished with slightly clavate feet and bristles of considerable length. Then follow the constriction of the alimentary canal (which Claparède does not indicate) and twenty segments, the first eight or nine of the series having still longer bristles than the foregoing division. The dorsal vessel (or vessels) sends powerful currents forward by regular contractions, which form a fold of the trunk opposite the fifth bristle-bundles.[2] The opaque white glands of the posterior part of the proboscis were distinct on capture, but they became less visible after confinement in the laboratory.

The Spio-like forms figured in Pl. 8, figs. 1 and 2, thus diverge from the unmistakable larvæ of Magelona figured by Claparède and in fig. 3 of the plate just mentioned in the present paper. They show no transverse striæ at the base of the tentacles, and the proboscidian region of the gullet is much shorter. Opaque white glands, however, occur at the sides of the latter posteriorly, and the arrangement of the eyes, the general contour and the number of segments in the anterior region of the body, are similar. Again, some examples agree with the two figured (Pl. 8, figs. 1 and 2), but have at the base of the tentacles indications of the rugæ which foreshadow the papillæ characteristic of the species in its adult

[1] Claparède (op. cit., fig. 10) figures the younger stage with a considerably larger snout than the later stage, a feature perhaps due to individual variation.

[2] In a dying specimen, somewhat smaller than the present form, a large pinkish oil-globule occurred in the anterior region—the product of decomposition of the blood or other fluid.

condition; but such have never presented at St. Andrews the long slender larval papillæ simultaneously in the same region, and which Claparède shows in his fig. 12. Though the young stages of allied members of the Spionidæ are not yet sufficiently known, yet the weight of evidence inclines to the view that the Spio-like larvæ pertain to Magelona, at a stage previous to the appearance of the rugose ridges ushering in the thick cylindrical papillæ. An interesting feature is the disparity in size between the latter examples without forward growth of the snout, and others, fully a third less, with a considerable snout.

On Claparède's Unknown Larval Spio.

The first notice of a form apparently identical with the larval Annelid which forms the subject of these remarks is given by Maximilian Müller,[1] who alludes to a fragment of the posterior end in connection with his observations on bacillary corpuscles.

When sojourning at St. Vaast la Hougue, between July and September, Claparède[2] found not unfrequently an unknown larval Annelid (pertaining to a common form) which has also occurred in considerable numbers in the bottom-nets at St. Andrews from July to October. The same form has been met with on the Norwegian coast at Christiansand.

The youngest stage measures about 0·045 mm., and has about twelve bristled segments, besides several without bristles. The head is short and is divided into symmetrical lobes. The ridge is richly ciliated, and differs from the arrangement in the larva of Leucodore. The larger bosses have short cilia and a pair of longer ones. The eyes are arranged more or less on a trapezoid (the posterior pair more widely separated), and have reddish pigment. The mouth lies on the ventral surface between two ciliated lobes. Two bands of cilia occur on the ventral surface behind the mouth. The first body-segment has a larger lateral process than the rest, and bears a long tuft of slender bristles, minutely spinose. The succeeding segments

[1] 'Observat. Anatom. de vermibus quibusdam maritimis,' 1852, p. 29, pl. ii, fig. 29.

[2] Op. cit., p. 77, Taf. vi, f. 1—11.

have shorter bristles. Each segment has a short tuft of cilia, somewhat resembling the ventral tuft in the Magelona-larva. The terminal segment is ring-like and bears long cilia. The alimentary canal is pale and wide, but constricted at each segment-junction.

An older stage with from eighteen to twenty-four segments showed dorsal and ventral foot-papillæ, and a pair of rudimentary tentacles on the head, the posterior part of which is elevated (as in Pl. 7, fig. 7).

When the larva reaches $2\frac{1}{2}$ to 3 mm., and has from thirty-five to fifty segments, the tentacles are longer and show an internal cavity, and the rows of cilia are longer, though shorter than in the larvæ of Leucodore. The lips are richly ciliated, and a tuft of cilia occurs on each side behind the head. The anterior pair of eyes are blackish, as in the older larvæ, whereas the posterior pair are reddish. The foot-processes are larger at this stage and somewhat conical. Moreover, a brownish speck occurs between them, whereas in the examples at St. Andrews it was whitish or yellowish white. The bristles have the same rough aspect (from minute spikes), and the first segment bears longer bristles than the following. In all the segments the ventral row of cilia is present, while posteriorly is the anal ring of long cilia. The pale alimentary canal contains sea-water. The larva wriggles through the water for some time and then settles on the bottom. It is translucent like Tomopteris, the only pigment being the coloured specks on the sides (between the feet).

When supplied with sea-water, development proceeded, the dorsal and ventral divisions of the feet from the seventh to the eleventh becoming longer, thicker, and with a slender tip, all the others remaining as before. Further, the dorsal branch of the foot showed reddish pigment, whereas the ventral remained pale. The opaque speck (black?) remains between them. By-and-by the long cilia of the lateral regions of the head and the anal ring disappeared. Moreover, the presence of the longer feet from the seventh to the eleventh segments was somewhat inconstant, for in one in which only thirty-five

segments existed they were well developed; whereas in another with forty-five to fifty segments they were not longer than the others.

The geographical distribution of this larva is extensive, and Claparède gives a figure of one from Christiansand which for the most part corresponds. He does not know any adult Annelid with longer feet from the seventh to the eleventh, nor with the peculiar spinose bristles, which are probably provisional organs The peculiarity is that they existed so long.

The most advanced larva procured by Claparède was thus only supplied with short tentacles, that is, little more elongated than in Pl. 8, fig. 4, of the present paper; whereas several procured at St. Andrews in October had these organs considerably elongated—stretching backward to the fifth (Pl. 8, fig. 5) and even to the eighth bristled segment. They are large and comparatively massive organs resembling those of the Spionidæ. The unpaired process in front is considerably shorter than that figured by Busch,[1] and Claparède and Mecznikow,[2] in the larval Nerine cirratulus. Perhaps it only develops in the later stages, for in Pl. 7, fig. 7, it is not visible in a lateral view. Moreover, several with long tentacles had shorter bristles than in the earlier stages. The tail terminates in a somewhat ovoid tip with a dimple in the centre and a ring of cilia towards the tip (Pl. 7, fig. 8). In lateral view, however (ibid., fig. 9), the tip occasionally assumes a conical condition. A dorsal and a ventral blood-vessel (Pl. 8, fig. 6) are evident in the same view (lateral). The conspicuous pigment-speck between the bases of the feet is either opaque white or yellowish white, and is often finely ramose. Towards the end of October (23rd) an advanced example had peculiar globules which refracted the light like oil along the lateral region (Pl. 8, fig. 7) from the tenth foot backwards. They were absent from both dorsal and ventral aspects till near the tip of the tail. Their

Beobachtungen üb. Anat. u. Entwicklung., &c.,' p. 65, Taf. viii, figs. 1—4.

[2] "Beiträge zur Kenntniss der Entwickelung. der Chætopoden," 'Zeit. wiss. Zool.," Bd. xix, separ. Abdr., p. 11, Taf. xii, fig. 4.

nature is doubtful, but it is possible they were due to degeneration, though the animal appeared to be active and healthy, the only feature of note being the great length of the bristles flanking the sides and the comparative shortness of the tentacles. Some of the advanced specimens were three-eighths of an inch long and had thirty-two segments behind the head.

The bristles of the long larval tufts in front seem to be more or less smooth in spirit-preparations. The minute spikes on the stronger bristles of the feet are readily seen. The bristles are generally in groups of three or four on each foot.

In section the cuticle is found of considerable thickness, and beneath is a feebly developed circular coat, then a boldly marked layer of longitudinal muscular fibres, arranged in two dorsal and two ventral bands. The long processes characterising the feet from the seventh to the eleventh segments have large hypodermic cells internally, with their long axes parallel to that of the process. The nerve-cords form two flattened granular bands on each side of the middle line ventrally. They have the hypoderm externally, and apparently a space over each internally. The oblique muscles pass to their outer edges, and probably go beneath them.

No further light has been thrown on the relationships of this form except that the tentacles in the most advanced confirm the opinion of Claparède that it pertains to the Spionidæ. It is apparently the larva of a species not uncommon at St. Andrews.

EXPLANATION OF PLATES 6—8,

Illustrating W. C. McIntosh's paper, "A Contribution to our Knowledge of the Annelida."

PLATE 6.

Fig. 1.—Longitudinal (horizontal) section of the caruncle of Euphrosyne foliosa, Aud. and Ed., behind and on a level with the eyes. × 350.

Fig. 2.—Vertical section of the caruncle, showing a somewhat radiate arrangement of the fibres in the organ, while inferiorly strong fibres pass from the trunk into it. × 55.

Fig. 3.—Vertical longitudinal section of the anterior region of the same species on one side of the median line, showing the muscular fibres, *m.*, passing to the caruncle, *car.* *ocd.* Dorsal eye. *ocv.* Part of a ventral eye. *c. g.* Cephalic ganglia. *v.* Section of blood-vessels. *w.* Mouth. *wf.* Anterior folds of the lining of the mouth. From the slightly oblique nature of the section certain of the anterior bristles, &c., are seen in front. × 55.

Fig. 4.—Transverse section of a branchial stem, towards the base. × 350.

Fig. 5.—Transverse section of the same organ, towards the tip. Zeiss, obj. D, oc. 1.

Fig. 6.—Vertical (transverse) section of a branchial stem as it leaves the surface of the body, showing fibres entering the region. × 350.

Fig. 7.—Vertical longitudinal section of the anterior end of E. foliosa. *bs.* Gastric chamber. *br.* Transversely ridged region, only a portion being seen in this section. *e.* Muscular ridges. *gl.* Glandular area. *w.* Mouth. *wf.* Folds of the buccal membrane. × 24.

Fig. 8.—Slightly oblique section (though more or less vertical and transverse) of the cephalic ganglia of Euphrosyne foliosa in the region of the dorsal eyes. × 55.

PLATE 7.

Fig. 1.—Vertical (transverse) section of the region of the caruncle in Euphrosyne cirrata. *a.* Vertical fibres from the ventral region, above nerve-trunks. *car.* Caruncle. *t.* Tentacle. The knife has passed through the caruncle after the central space has disappeared. The section is probably more or less oblique. × 55.

Fig. 2.—Slightly enlarged view of a softened example of Euphrosyne foliosa, with the alimentary canal exposed. *a.* Anterior glistening region of the proboscis. *b.* Dorsal continuation of the canal. *c.* Striated or ridged muscular region. *d.* Pyloric part of the passage *b.* *e.* Intestine.

Fig. 3.—Vertical transverse section of the proboscidian stem near the glandular region. A thin line cuts off a lateral area at each side. *bs.* Alimentary canal. × 80.

Fig. 4.—Vertical transverse section of the anterior ventral region. *ba.* Wall of intestine. *n. c.* Nerve-cords. *c. m.* Circular muscular coat; the same letters mark the nerve-commissure. The oblique fibres decussate beneath the nerve-trunks, and join the circular coat. Sections of vessels are seen at *v.*

Fig. 5.—Transverse vertical section of the anterior region, where the canal, *bs*, from the gastric region joins the intestine, *ba.* *vd.* One of the dorsal trunks. *vg.* Central dorsal vessel. *gp.* Reproductive elements—in this case male. × about 60.

Fig. 6.—Transverse vertical section, anterior to Fig. 5. The dorsal vessel has now split into two trunks, *vg*. Zeiss, obj. A, oc. 1.

Fig. 7.—Head of Claparède's larval "Spio" of 16th July. × 52.

Fig. 8.—Posterior end of the foregoing form, in a specimen procured in October (?). × 52.

Fig. 9.—Lateral view of the tip of the same example. × 52.

PLATE 8.

Fig. 1.—Young form resembling Magelona papillicornis in which the head has not yet extended beyond the tentacles, and in which the long larval bristles are present anteriorly. *a.* Constricted region of the alimentary canal. *gl.* Glands of the pharyngeal region. The anterior region of the alimentary canal is distended with water. 28th May. × 55.

Fig. 2.—A similar specimen after the long larval bristles have been shed, and viewed from the ventral surface with the tentacles fully extended. × 55.

Fig. 3.—A more advanced example, in which the basal part of the tentacles has larger papillæ, and the snout has considerably increased in size; yet the long larval bristles are still present. 17th October. × 50.

Fig. 4.—Dorsal view of the anterior region of Claparède's larval "Spio" of 16th July. *ph.* Pharynx. × 52.

Fig. 5.—Anterior end of the most advanced form of the same species yet found. The tentacles are considerably larger. 23rd October. × 52.

Fig. 6.—Lateral view of an example of the foregoing, showing the chromatophores and feet. 16th July. × 52.

Fig. 7.—A similar view of a specimen (23rd October), in which peculiar refracting bodies, like oil-globules, occurred along the lateral aspects. × 52.

Spolia Nemoris.

By

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With Plates 9—12.

It was in the summer of 1889 that an invitation reached me, coming from the Royal Physical Society (Koninklijke Natuurkundige Vereeniging) in Batavia, to undertake a trip to the Indian Archipelago for purposes of scientific research. This invitation opened the prospect of realisation of a wish long cherished and for a naturalist not exorbitant,—the wish to have a direct glimpse and a personal impression of animal and vegetable life in the tropics. And so it was accepted with alacrity.

Now that I am going to give a summary account of my investigations during this temporary sojourn in India, the results of which are gradually taking a shape that will permit of their successive publication, I cannot refrain from expressing my grateful indebtedness to the above-named Society and to its Council. Although the funds that were required for these researches have been granted by the Government, to whom I am for that reason equally indebted, still it was the Society who transferred the responsibility for the way in which the money was to be spent entirely to me, with what I would be inclined to call a blind confidence.

In consequence of this I was quite free in the choice of any research I might wish to undertake, and also in the method

according to which I should desire to conduct both the collecting and the working out of the subject-matter of these investigations. I resolved to extend certain researches with which I had been occupied for the last few years, and which had reference to the earliest developmental stages and the formation of the germinal layers of mammals, as well as to the numerous and often unexpected points of difference which we observe in the first origin and in the detailed anatomy of the placenta (afterbirth) of different mammals.

Of late years the mammalian placenta has been more closely studied by numerous anatomists, but nevertheless its highest stage of differentiation as found in the human subject is yet so imperfectly understood (genetically) that a comparative investigation of the more primitive orders of mammals is an imperious necessity. As in all other attempts at comparative analysis, so in this case the selection of the material that is to furnish the bases of comparison is most important.

Now the lowest mammals (Ornithodelphia, Didelphia) are as yet deprived of a placenta; this organ has only become developed in later, more highly differentiated orders. It is thus the very youngest organ which we meet with in mammals, the latest acquisition by the gradual perfecting of which they have obtained a considerable advantage over the lower Vertebrates.

The order of the Insectivora is regarded as being the most archaic among the Mammalia Placentalia, both on account of palæontological and of anatomical data. And so the objects of comparison had to be chosen in the first place among these more primitive forms.

Several years ago I commenced to study the process of placentation in three European representatives of the order Insectivora—the hedgehog, the mole, and the shrew,—and have published part of the results of these investigations.

In the Indian Archipelago other genera of the same order occur which are entirely absent in Europe. Towards these my attention had in the first place to be directed during my stay in the Archipelago. They are the genera Tupaja and Gymnura, of which the latter very soon proved too rare to be

available for this investigation. Tupaja, on the contrary, is much more common, and I might safely feel hopeful to collect a rich harvest of Tupaja javanica.

Besides the additional genera of the order of the Insectivora, the investigation had in the second place to be directed towards another order which is said to occupy an intermediate place somewhere between the Insectivora and the highest order, that of the Primates, to which man and monkeys belong. This intermediate order is that of the Lemuridæ or Prosimiæ. In Europe it is no longer represented by living genera, although in earlier geological periods it did occur in this part of the world. A small number of genera compose this order, by far the majority of them being found in Madagascar.

Two representatives of the Prosimiæ occur in the Indian Archipelago, viz. Nycticebus and Tarsius. A peculiar genus of mammals, the so-called flying maki or Galeopithecus—different in organisation as well as in mode of life—was at one time regarded by zoologists as being more closely allied to the Lemurs, at another time to the Insectivora or to the Cheiroptera, or even as an order by itself (Dermoptera). This genus also occurring in the Indian Archipelago, it had similarly to be included in the sphere of the projected investigation.

Finally, I was interested in the only representative of the order of the Edentata that has as yet been brought to light in the Indian Archipelago, viz. Manis javanica, and desirous to obtain a complete series of the different stages of placentation of this animal; the Edentates presenting considerable differences among themselves with respect to their placentation.

Coloured drawings of the above-named mammals were distributed, a few months before my arrival in India, by the Royal Physical Society amongst a number of persons with whom readiness to co-operate appeared probable.

To this was added a circular, answers to which successively arrived. My friend Dr. P. C. Sluiter, librarian to the Society, to whose energetic assistance I am deeply indebted, entered into a preliminary correspondence with the writers, and placed

the outcome of this at my disposal when I arrived in Batavia in November, 1890.

In this way matters were made easy for me, and I could form a provisional opinion as to the question in which part of the Archipelago I would probably find the most favorable collecting spots.

Only certain general data were available as to the habitat of the above-named genera of mammals, but detailed accounts about their comparative rarity, by which certain regions might at the outset be considered as less favorable than others, were deficient, as were also reliable data about their time of reproduction, &c.

Moreover, different aspects of the question must be kept sight of. Suppose the animals to be numerous in a region without European inhabitants, I could not then expect a rich harvest. Similarly it might be presumed that in parts where the population is scarce, the inhabitants could hardly give any important aid in the collecting of a great number of specimens.

On the contrary, it was most probable that in strongly populated districts where a large proportion of the soil is cultivated, the mammals in question would be very rare or extinct. It was, in short, unavoidable to spend the months of my stay in India in as considerable a number of different places as possible. In this way I was able to enter into personal connection with very many who might be willing to continue the collecting business even after my departure. For this purpose I left behind me, wherever I had succeeded in enlisting co-operators, printed instructions, chemicals, glass tubes, &c., as well as cash for the payment of premiums to the natives by whom the collecting of the live material was to be done.

This method of going to work must appear to be a tedious and slow one. At the same time it was in the commencement most undoubtedly disheartening. Still I have conscientiously applied it wherever I have stayed, after generally demonstrating by means of more common animals than those I was in search of how the extirpation of the uterus had to be effected,

and how the preservation was to be done. Now that three years have passed by, I may safely say that the results have far surpassed my expectations.

Among the hundreds of persons with whom these roamings through the woods and mountains of Java, Sumatra, Banka, Billiton and Borneo have brought me into close connection, and who have been interested in the object of my investigations as explained to them by me, it is only natural that the great majority has been unable by various circumstances to contribute in any way towards the increase of my embryological collection.

They, however, who have thus contributed can hardly have imagined how their apparently small collections—but which are being forwarded from numerous parts—can together constitute a very considerable array of important material for research. Such has undoubtedly been realised on this occasion, considering that at this present moment I already dispose of—

469	uteri of	Tupaja,
137	„	Nycticebus,
72	„	Galeopithecus,
198	„	Tarsius,
150	„	Manis,

making the respectable total of 1026. This collection is yet increasing continually by new arrivals.[1]

The majority of these uteri are pregnant in one stage or the other; many have been preserved very shortly after parturition; only a very few are virginal.

The pregnant uteri contain the most divergent stages, from the earliest phases of segmentation to the nearly ripe or newly born fœtus. Several newly born young have also come into my possession, as also a few in the very act of birth, the nearly born fœtus being still connected by its umbilical cord with the as yet adherent placenta.

The numerous microscopical preparations which have already

[1] While correcting this proof, new arrivals have again increased this total to 1072.

been made of the rich and varied material demonstrate the perfect care which most of my correspondents have bestowed on the preservation. Consequently the histological details of the placentation process, of the formation of the germinal layers, and of the ontogenesis can be studied from these preparations quite as satisfactorily as if the preparations had been freshly made in the laboratory.

Again in this respect Kleinenberg's mixture (picro-sulphuric acid) has proved to answer to a very high standard of excellence; in the case of the preservation of uteri *in toto* it gives the best chances for the finer details of early blastocysts therein enclosed, or of the placentary structures in the course of formation, to be perfectly preserved; always on this sole condition, on which I have everywhere laid particular stress, that the extirpation be made instantly after death. Preparations made from animals that had been dead even for only a very short time have already undergone so considerable an alteration that they are of very inferior value for comparative and especially for histological research.

A point which had more particularly puzzled me before I commenced my peregrinations was the question at which period of the year the animals I was going to search for reproduced their species. As was already noticed above, the literature on the subject leaves us entirely in the dark with respect to this point. And though the alternation of seasons is much less marked in the tropics than in the temperate regions, still the regular succession of the "rainy" monsoon and of the "dry" monsoon—more marked, however, in certain parts of the Archipelago than in others—might be expected to have a certain influence on the birth-rate and on the association of the sexes in these animals.

If in the commencement I have been inclined to believe that it would be possible to detect any such parallelism, still, as the collections have increased, it has become more and more evident that reproduction of the species investigated occurs all the year round.

In the same months the most divergent stages of pregnancy

have been observed to occur; in no month have they been deficient. My different correspondents have come to the same conclusion as soon as the material they brought together became more extensive, and allowed them to compare the results of different months.[1]

Another general conclusion, which has more especially been verified for Tupaja and Tarsius, is that pregnancy is repeated at rapid intervals, very early stages of development being often found in the same uterus simultaneously with the yet indubitable remains of a preceding pregnancy, as judged from the unmistakable traces of a preceding placentation, from the nature of the uterine wall and the uterine vessels, &c.

In the case of Galeopithecus it twice occurred that a young animal was yet being suckled by the mother and was found attached to her breast, whereas autopsy showed an already fairly advanced younger fœtus to be present in the uterus of the same specimen.

The fact that all the species here mentioned bring forth only one young at a time (Tupaja, which regularly carries two fœtus simultaneously, alone excepted) may perhaps account for the prolific properties here referred to, being developed as a counterbalancing agency to this restriction of the number contained in one litter. In our European Insectivora, whose time of reproduction is limited to only a few months or even weeks in the year, the litter normally amounts to eight (Sorex) or six (Erinaceus, Talpa) young ones.

Of all the cases that have as yet come under my observation I know of only one case of twins in Nycticebus. They were enclosed each in a different horn of the uterus, whereas in the normal cases one of the two horns is always barren.

In Tarsius, Galeopithecus, and Manis I have never noticed more than one young at a time. In Tupaja never more and

[1] It should be here noted that I have on more than one occasion heard it reported by sportsmen and natives that for the Indian deer, periods of heightened and lessened sexual activity do exist. I will by no means generalise any further than my acquaintance with the species here investigated will allow me to do.

never less than two are present, occupying the right and the left half of the uterus.

There, as formerly in Sorex, I have, however, been able to establish without doubt that the number of fecundated eggs and even yet of early blastocysts is constantly found to be more considerable than the number of ripe fœtus that attain maturity and form the normal contents of a litter.

Thus in Tupaja four and sometimes more blastocysts are found in early stages, apparently all of them in equal conditions of vitality. A struggle between these blastocysts for the definite attachment to the maternal uterine wall is thus inevitable. How this struggle is brought about and what points finally decide between those that shall thrive and those that shall perish is at present obscure. Still the fact has no doubt a definite significance, considering that it is not a casual observation, but a most regular occurrence in at least two genera of Insectivora.

My preparations are not yet numerous enough to allow me to speak with the same emphasis for the other genera.

Attention will of course have to be directed to this point, in order to make out whether it may be regarded as a general rule in mammals that more blastocysts than can partake in the normal course of intra-uterine development are present in the earliest days after fecundation has taken place.

One question to which my preparations do not allow me to reply is that concerning the duration of pregnancy in the five species investigated. The lapse of time that occurs between the date of fecundation and that of parturition is in no way indicated even by the most complete set of intermediate stages between the cleaving egg and the ripe fœtus. On the other hand, it is in no way of any importance for the correct interpretation of the different and successive ontogenetical processes to be acquainted with the exact rate at which these stages succeed one another, or with the age of any particular stage as expressed in a fixed number of days.

With animals bred in domesticity this is of course easily

accomplished. But then, on the other hand, the domestic animals have in later years been often shown to furnish us with data that are more liable to a certain amount of divergence than those which have been obtained from animals living in absolute freedom. There can hardly be a doubt that the inevitable pammixia which accompanies domestication can alter and render variable parts of the organism both internal and external, which have a more fixed standard in their non-domesticated congeners.[1]

For this reason the study of mammalian ontogeny, not from the rabbit and the Cavia, but from specimens of other species and genera captured in their natural haunts, deserves special recommendation.

The object of this paper being to establish certain general facts that come to light when the pregnant stages of the five genera in question are compared macroscopically, and before the microscope is as yet brought to bear on the numerous and intricate questions of histological detail, it will recommend itself to treat the five genera separately.

Tarsius spectrum. Figs. 1, 2, 18—21, 47—49.

There can be no question that all the specimens obtained by me belong to Tarsius spectrum, Pall., and not to Tarsius fuscomanus, Fisch. The differences between these two species have lately been fully discussed by Weber in vol. iii, p. 260, of his 'Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien,' Leiden, 1893. None of the uteri in my collection were obtained from the localities to which Tarsius fuscomanus is restricted. The name by which Tarsius is known to the natives in South-west Sumatra is singo puar; those of Banka call it the berook puar, or mentiling; those of West Borneo, tempiling.

[1] Renson, 'Contribution à l'embryologie des organes d'excrétion des oiseaux et des mammifères,' Bruxelles, 1883, p. 37.

C. K. Hoffmann, "Die Bildung des Mesoderms, &c.," 'Verh. v. d. Kon Akad. v. Wetenschappen te Amsterdam,' 1883, p. 2.

J. v. Erp. Taalman Kip, 'De ontwikkeling der Müllersche gang by de zoogdieren,' Dissert. inaug., Utrecht, 1893, p. 77.

In a yet higher degree than the other Prosimiæ, Tarsius was recognised by the older anatomists to be intermediate between Insectivora and Primates. Burmeister, in the preface to his 'Beiträge zur näheren Kenntniss der Gattung Tarsius,' writes as follows (p. 6) :—" Tarsius possesses, in addition to its considerable external similarity to monkeys, the most complete insectivorous dentition which Quadrumana can boast of, for even the incisors have adopted the type of the canines, and have thus become eminently like the true dentition of the Insectivora. In this Tarsius differs from all other Prosimiæ."

The non-pregnant uterus of Tarsius has been figured on pl. 6, fig. 22, of the above-mentioned work.

The author thus describes the internal female organs :— " They consist of two small ovaries, the coiled oviducts, and the two-horned uterus. . . . The ovaries are small spherical bodies, half a line in diameter; their surface is quite smooth, and their inner substance is of the ordinary condition of that of the higher mammals. . . . The uterus is two-horned, each horn being three inches long; then follows the unpaired portion, which attains to half an inch, and externally passes into the vagina without any interruption. On the inner surface I could, however, detect a faint boundary as an ostium uteri. The uterus horns, as well as the unpaired portion, have thick walls, and show numerous considerable folds."

I have now before me several dozens of non-pregnant and early pregnant Tarsius uteri, and I have little to add to Burmeister's observations. There is, however, very often a strongly marked difference in size between the two ovaries, one swelling up to the size of a pill, the other remaining considerably smaller. I was inclined to believe that this difference in size might go parallel with fecundation, and thus indicate the presence of an early developmental stage in a uterus with one of the ovaries thus swollen. Series of sections in which the uterus lumen and that of the oviduct have been most carefully scrutinised, oblige me to give a negative answer to this conjecture. The cause of this swelling of one of the ovaries was investigated, and will be treated of elsewhere. It was

more than once noted in the fresh animal before preservation by one of my correspondents, to whom I am indebted for most valuable material.

Concerning the aspect of the internal genital organs of Tarsius when fresh and in situ, he tells me that the colour of the ovaries is often very different. Sometimes pink, they are at other times of a lighter and darker yellowish hue; and in young specimens they have the appearance of a small row of spherical or rod-like bodies of a light yellow colour. I have not yet found time to study the sections of the young stages of the ovaries thus characterised.

The body of the uterus with its double horns of the preserved specimens in my possession is extremely variable in shape according to circumstances. It is difficult to detect the very early stages of pregnancy at first sight.

Yet long before the embryo has proceeded so far that the medullary groove has made its first appearance on the surface of the blastoderm, there is a very marked swelling of the uterine half in which the blastocyst has come to adhere.

This uterine swelling is in no way perfectly spherical, but more saddle-shaped, in accordance with the fact that even in these early stages the blastocyst adheres to the maternal tissue in one particular region, and not along any more extensive surface, as, for example, in the shrew, the mole, the hedgehog, &c.

The details of this process will be fully described elsewhere. I may here add that this early point of attachment corresponds in situation to what will, in a later stage, become the placenta, and that no omphaloidean attachment precedes as a temporary structure the definite placentary connection.

When pregnancy advances it can be noted that the placenta does not occupy a varying but, on the contrary, a fixed position with respect to the different regions of the uterus. It is always situated close to the apex of the horn on the mesometrical side, and the swelling of the uterine walls is not most conspicuous close to this point of attachment, but more towards the vaginal portion of the horn (cf. fig. 1). It is in this more extended part of the uterus that the head of the full-grown fœtus is

situated, which is thus normally the first to pass outwards at birth (cf. fig. 18).

When a uterus containing a ripe or nearly ripe fœtus is carefully opened by a longitudinal incision, there is seen to be no adhesion whatever except in the placentary region (figs. 18—21). The uterine walls are stretched to an extreme degree of tenuity; indeed, so thin have they become that even in the specimens that were preserved in spirits, and have thereby considerably increased in opacity, the limbs, the ears, the fingers, and the tail of the fœtus can be distinguished through this thin layer of maternal tissue.

Immediately beneath the stretched uterine wall the fœtal envelopes form a very tight sac containing the fœtus. This sac is so transparent that in spirit specimens the individual hairs on the head, body, and limbs, the nails, &c., can be recognised through it (figs. 18 and 47).

Towards the tail end of the fœtus the fœtal envelopes pass into a button-like projection, which constitutes the placenta. Figs. 18, 19, and 47 show this both in the front view and in profile; in fig. 20 the longitudinal section indicates still more clearly the way in which the thin fœtal envelopes merge into the placentary tissue. It is, moreover, visible, both in fig. 18 and in the longitudinal section (fig. 20), that the placentary knob itself adheres with the maternal tissue only along a very limited extent of its total surface, viz. a squarish area in which numerous lumina are visible (figs. 18 and 47), when the placenta is loosened from the maternal tissue by a slight shaking. These lumina are formed by the tracts which convey maternal blood to and from the placenta. Microscopical examination of thin sections through this region reveal without any doubt that, indeed, this limited area is the only point of fusion, the remaining surface of the placenta being as little fused with the maternal tissues opposite to it as are the fœtal membranes themselves. About the histology and the genesis of the placenta of Tarsius I will treat in a later paper; suffice it to say that, according to the nomenclature now in use, the Tarsius placenta would be directly classed with the discoid

type. It has not the faintest trace of any relation whatever to the diffuse type, which was hitherto considered as being the type of placenta to which the Lemuridæ belong.[1]

The umbilical cord by which the embryo is connected with the placenta is comparatively short; it is represented in figs. 20 and 21, containing very prominent vessels.

In fig. 21 the ramification of these vessels on the placenta is, moreover, indicated as this is seen (in a spirit specimen) after the removal of the fœtus. Fig. 49 represents the fœtal membranes and the placenta with severed umbilical cord after they have been removed out of the uterus, and the fœtus has passed out of its envelopes.

These envelopes having here been preserved after the fœtus had been expelled are less stretched and transparent than those of figs. 18 and 47. The afterbirth of Tarsius (which is expelled in the customary way and not resorbed in situ, as that of Talpa) consists of these same parts; the envelopes are then more folded together against the knob-like placenta than in fig. 49.

Embryos of Tarsius are in my possession from the earliest stages of segmentation up to the newly born young. Two of them are represented in figs. 46 and 48. In the first the comparatively large size of the head is worthy of note; in the second the way in which limbs, fingers, and tail are tightly folded together against the body in a small compass deserves special attention.

The details of the ontogeny of Tarsius, which as yet has never been investigated embryologically, I hope to be able to work out soon with the aid of the very complete material now at my disposal.

With respect to the details of the placentation process I will also have to refer to a later publication, and can only state that the trophoblast of the very early two-layered blastocysts undergoes a most considerable amount of proliferation at the spot where the uterine surface has in its turn undergone certain

[1] Cf. a preliminary notice in the 'Procès Verbaal van de Koninkl. Akademie van Wetenschappen te Amsterdam,' Zitting van 2 April, 1892.

differentiations intended for the future attachment of the blastocyst. This proliferation, the products of which undergo remarkable further developmental changes, eats its way very deeply into the maternal tissue between the tubular uterine glands.

Vascularisation of this proliferated region, which fuses in a particular way with the surrounding maternal elements, is then brought about, for maternal blood circulates in it freely and copiously, and soon another system of vascular channels connects the growing embryo with this rich source of energy.

A very early and profuse growth of mesoblastic tissue plays an important part in this secondary connection between the growing fœtus and its chorion, and accentuates in a suggestive way the several features by which Tarsius approaches the Primates.

However, I shall have to postpone a detailed description of this point to a later publication.

Nycticebus. Figs. 3—5, 22, 23, 30—40, 50—56.

This second genus of Prosimiæ, represented in the Archipelago by the species Nycticebus tardigradus and N. javanicus,[1] is known by a series of names which have much the same sound, but in which the consonants vary according to the different regions. These names are—kukang, tukang, pukang, and huhang. In East Sumatra and Banka the name of berook semoendi is in vogue among the natives. In East Java specimens were especially difficult to procure because the skeleton is said to be most efficacious in bringing about death and destruction among the unfortunate inhabitants of a house in front of which it has been buried overnight. It is thus in high

[1] Of this species I have obtained but very few specimens in East Java, and no pregnant uteri. Although no specific determination was ever made by those who so kindly collected and preserved the uteri at present available, I have no doubt that they all belong to the only species which is known to occur in the islands from which my collections have come (Sumatra, Banka, and Borneo), viz. Nycticebus tardigradus.

demand among the wealthier natives who have family quarrels to settle, and I have known exorbitant prices, with which a collecting embryologist could not possibly compete, to be stealthily paid for one specimen, for this unfriendly though perhaps harmless purpose.

As will be seen, Nycticebus differs most considerably from Tarsius in several important respects.

The stages of pregnancy, as studied from the unopened uterus, are not characterised by any very marked peculiarity. In the three uteri figured on Pl. 9 the ovary is seen to be more or less concealed by a mesenterial fold, which contains the Fallopian tube, whereas the two horns of the uterus have a peculiar asymmetrical shape, being rounded dorsally and pointed ventrally. This latter detail, which can be easily recognised in the uteri that are young or in early stages of pregnancy, is of course lost as the swelling of the pregnant horn increases. Still, even then it can yet for a very long time be detected in the non-pregnant horn.

In the literature on the Mammalia I do not find any other representation of the uterus of Nycticebus than those contained in Kuhl's "Einiges über die Splanchnologie von Stenops gracilis" (Beiträge zur 'Vergl. Anatomie, zweite Abtheilung,' p. 37, pl. 6, Frankfurt, 1820); and in Schroeder van der Kolk's papers, 'Bijdrage tot de Anatomie van den Stenops kukang' ('Tijdschrift voor Nat. Gesch. en Physiol.,' vol. viii, pl. 5, figs. 8 and 9, Leiden, 1841). This latter figure is most insufficient, and does not in any way indicate the peculiarity just mentioned. Moreover in these figures other peculiarities—for example, an abnormal extremity of the Fallopian tube (l. c., fig. 9)—are represented, and a total absence of fimbria is noticed which does not conform to the actual facts, and which differs markedly from what figs. 3 and 7 teach us. V. d. Kolk's specimens must have been somewhat mutilated and perhaps imperfectly preserved.

The first pregnant uterus of Nycticebus which I opened was the object of particular expectancy. Knowing that for the Madagascar Lemuroids (Propithecus, Indris, Avahis) both

Milne Edwards[1] and Turner[2] had described and figured a diffuse placenta, which was, however, first distinctly recognised as such by the latter, and that Tarsius in this respect reveals such a totally different arrangement, it was of course of a double interest to know whether Nycticebus would conform with either of these types, or would represent one by itself.

The first dissection which I ventured to make was for this reason effected with special precautions. It is represented in figs. 22, 30, and 36, and from the first of these three figures it will be seen that, to begin with, the muscularis was carefully peeled away. The outer surface of the mucosa thus brought to light revealed (by transparency) the presence of a network, the meshes of which are visible to the naked eye. The character of this network could be better recognised as soon as the incisions had been made that are represented in fig. 30, *M* being the same flaps of the muscularis that are indicated in fig. 22.

The mucosa (*m*) was seen to present projecting ridges arranged in reticular fashion, and between which polygonal areas were thus enclosed, into which villiform protuberances of the underlying fœtal envelopes were seen to fit. So loosely did they fit, however, that no traction whatever was required to sever the connection between chorion and mucosa all along this spherical surface. The fœtus with its envelopes could be floated out of the mucosa the moment the preparation represented in fig. 30 were to be turned upside down.

The reticular surface of the mucosa is seen in a much more natural connection of the parts in figs. 23, 31, and 32, where the uterus has been opened and the flaps cut out of the wall have been folded back. The mucosal network and the muscularis have here remained unseparated. Still it was quite as easy to remove them from the subjacent fœtal envelopes as it was in the foregoing case.

[1] A. Milne Edwards et A. Grandidier, 'Histoire Naturelle des Mammifères de Madagascar,' Paris, 1875.

[2] Turner, "On the Placentation of the Lemurs," 'Philosophical Transactions of the Royal Society,' 1876, p. 569, pls. 49—51.

And so all these preparations leave no doubt that with respect to the connection between mother and fœtus Nycticebus resembles ever so much more closely the Madagascar Prosimiæ than it does Tarsius.

However, there are differences between the Madagascar genera and Nycticebus that deserve special mention. Firstly, the maternal network in the former (Milne Edwards, l. c., pl. 114, fig. 1) is much less decidedly reticular, and, on the contrary, more lamellar than what is here represented (figs. 38, 51, 52, 56) for Nycticebus. Turner's figs. 6 and 8 (also taken from Madagascar lemurs) agree very closely with those of Milne Edwards. Secondly, the outer surface of the fœtal envelopes is very much the counterpart of the maternal arrangement, as can more especially be seen from Turner's figs. 3, 4, and 12; but also from Milne Edwards' pl. 114, 117 (3), and 118 (1). And in this respect Nycticebus presents the same phenomenon of concordance between the fœtal excrescences and the maternal crypts, so that, instead of the lamelliform arrangement of the chorionic surface so conspicuous in the Madagascar lemurs, we here find circumscribed short columnar villi, each one of them fitting into a corresponding depression of the maternal reticulum. These columnar villi are quite equally distributed over the whole surface of the chorion, as is more particularly indicated in figs. 23, 31, 50, and 53. As pregnancy draws to its close, these chorionic villi disappear on a restricted chorionic area, which covers the head of the fœtus and is directed towards that side where the corpus uteri and vagina are situated. The maternal surface opposite this part of the chorion is similarly non-reticulated. A flattened projection of the chorion, similarly without villi, is sometimes found attached to this anterior surface of the chorion. Both on the latter and on the projection here alluded to we find that the epithelial recesses, which will be mentioned lower down, are, all the same, present. The greater part of the chorion just before birth is, however, densely covered with the particular villi that indent into the maternal reticular crypts. The transitional region between the areas is represented in fig. 55.

In fig. 35 the fœtal envelope is seen in natural size, and between the villi numerous openings (*ap.*) are detected. In the earlier stages these openings are also already present, and can be easily seen with a lens or even with the naked eye. If we open the chorion enveloping the fœtus (fig. 30) we find the inner surface of what was the villiferous covering of the fœtus to be flat, and this inner surface to be only here and there interrupted by round patches (*R.*), each of which corresponds to one of the openings (*ap.*) just mentioned. Of these relations of the parts, figs. 30, 32, 34, and 36 give further elucidation, whereas the definite proof of the correspondence of the flattened and faintly prominent recesses (*R.*) with the apertures (*ap.*) can of course be more especially obtained in sections, as that of fig. 39.

The distribution of vessels on the inner surface of the chorionic envelope is more particularly visible in fig. 34; the attachment of the umbilical cord to the same in figs. 32, 33, and 36.

The villi themselves are at first (fig. 50) more cylindrical; when they increase in age they become folded and wrinkled to a not inconsiderable extent, as is visible in figs. 37 and 37 *a*. It may be expected that these folds and wrinkles correspond to coordinated arrangements of the reticular layer of the mucosa, the two thus fitting together in a very simple way.

The maternal folds on the mucosa are in the Madagascar lemurs interrupted at regular distances by small bald patches, both according to Turner (l. c., figs. 6, 8, and 9) and to Milne Edwards (woodcut on p. 280).

In these spots the tubular uterine glands open out between the folds that have arisen on the inner surface of the uterus in the course of pregnancy. In Nycticebus I find a more equal distribution, the gland openings being found in the centre of nearly every separate compartment of the reticular arrangement. In fig. 38 this is indicated, the darker shading at the bottom of these compartments representing gland tracts.

Viewed with a pocket lens the openings are often visible as a whitish spot near the middle, where they appear to be more concentrated.

Figs. 39 and 40, drawn with the camera with very low power,

give the exact relation of the maternal and the embryonic parts in a section through chorion and uterine wall. Of the latter, muscularis and mucosa are indicated in fig. 40, the elevated ridges of the mucosa that form the peculiar reticulum referred to being visible as so many inward projections. They are all covered by an epithelium which even in this far advanced stage can be readily distinguished. Immediately below this epithelium numerous finely branched maternal blood-vessels take their course, in every respect comparable to those which both Turner and Milne Edwards have made out by injections for the Madagascar Lemuroids.

The chorionic villi of Nycticebus are seen to fit very exactly into these cryptiform spaces; it is worthy of remark that the epithelium on the villi is in many places ever so much thicker and more considerable than what is found on the opposite maternal surface.

In the villi numerous embryonic capillaries take their course immediately below the epithelial layer. The two vascular surfaces are thus separated only by the thickness of two cell-layers, of which the maternal one is less high and less columnar.

The above-mentioned recesses (*R.*) in the chorion are clothed by a direct continuation of the chorionic epithelium. Smaller vascular villi with a much less massive core of connective tissue stand out into the lumen of these recesses, as can be seen both in fig. 39 and fig. 40.

The amnion which enshrouds the fœtus has been partly removed in fig. 30, and is partly folded back (after removal of the fœtus) in fig. 32. Also in figs. 36 and 54 it has been dissected away, whereas in these two latter figures the connection between the fœtus and the villiferous chorion by means of the umbilical cord is still retained, the chorion being partly inverted in the act of stripping off the embryo.

In the preparations here figured no indication is given of the yolk-sac and the allantois. In Milne Edwards' figures of Madagascar lemurs a very conspicuous place is allotted to the allantois, which he has inflated, and which thus showed digitate processes and a multilobulate shape. It is thus described as

being non-vascular. The exact terms of Milne Edwards are the following (l. c., p. 283) :—" Les parois de l'allantoïde sont délicates et transparentes, aucun vaisseau ne s'y distribue. Si l'on injecte un liquide coloré dans le pédoncule de cette enveloppe membraneuse on peut le suivre dans l'ouraque, à travers le cordon ombilical, jusque dans la vessie urinaire; preuve manifeste que cette poche, malgré ses caractères anormaux, représente exactement l'allantoïde des autres mammifères."

The above description would suggest that in the Madagascar lemurs the allantois plays a part which is to a certain extent comparable to what Selenka[1] has described for Didelphia (l. c., pl. 16, figs. 1—5, pls. 17, 18). But then in Didelphia it is the yolk circulation by which the chorion is vascularised, whereas in Milne Edwards' lemur fœtus he finds the umbilical vesicle to be extremely reduced. Traces of it can only be made out in embryos of very early developmental stages.

This latter fact shows that a comparison with the Didelphia does not carry us very far. The vascularisation of the chorion of the Madagascar lemurs must be a phenomenon sui generis if Milne Edwards' observations are confirmed; and it will be understood that for this reason an exact insight into the state of affairs as they present themselves in Nycticebus is all the more desirable, especially if all the genetic stages be closely followed, as the now available material promises to admit of.

This will at the same time explain why I wish to refrain from further discussing the point on this occasion.

Still I may be allowed to refer to an earlier publication in which I have insisted on the advisability of restricting the use in mammalian embryology of the name chorion.[2] I have there argued at some length why I proposed " henceforth to restrict the use of the term chorion to man, and—dependent upon

[1] 'Studien z. Entwickelungsgeschichte der Thiere,' Heft 4, "Das Opossum," p. 136.

[2] "The Placentation of Erinaceus europæus, &c.," 'Quart. Journ. Micr. Sci.,' vol. xxx, 1889, p. 382.

future researches—perhaps to the Primates." What Selenka has since made known with respect to monkeys, indeed, shows a close resemblance between man and certain monkeys with respect to these placental phenomena.[1] And I would now venture to insert in the above citation, after the word "Primates": "and to the Prosimiæ."

In accordance with this it will be seen that in the present paper I have used the term chorion a few times only in reference to Nycticebus and Tarsius, whereas with respect to the other mammals I prefer to employ the term "diplotrophoblast" (l. c., p. 385). It is thereby testified that a fœtal envelope is present which is only secondarily vascularised, either by the vessels of the allantois or by those of the yolk-sac.

And thus, for the present, the new data here adduced for Nycticebus are restricted to the fact that the embryo of Nycticebus is enclosed in a complete sac which is entirely covered with thick villi, and which is very loosely attached to the vascular meshes of the mucosa into which the villi fit.

I hope to be able to furnish ample information concerning the ontogenesis of the chorion, &c., in a later publication.

A short reference to the two figures 55 and 56 should yet be made. Fig. 55 is an enlarged photograph of part of the same preparation represented in fig. 35. The actual shape of the villi, their flattening and partial disappearance towards the right extremity, is here better visible than in the lithographic figure.

Fig. 56 shows very graphically what becomes of the earlier network of the mucosa that was represented in fig. 51. The frilling of the border of the ridges, which is not yet present in the latter preparation but which becomes conspicuous in the later phases of pregnancy, is better brought out in this photograph than in the still more enlarged fig. 38.

The big folds that are visible in fig. 56 have arisen in consequence of an intentional folding backwards of the uterine walls.

All around the central depression the reticulation is less

[1] 'Studien z. Entwickelungsgeschichte der Thiere,' Heft 5, pl. 35, fig. 11; pl. 36, fig. 5.

marked. Where the mucosa faces the flattened surface at one of the poles of the chorion above alluded to, the reticulation is also deficient.

Galeopithecus. Figs. 6—11, 24—29, 57, 58.

Concerning the ontogeny and the placentation of Galeopithecus, I could find no data in the mammalian literature but a few lines in an article of Gervais[1] on the cerebral conformation of the Mammalia (l. c., p. 425). He does no more than mention the fact that he examined a fœtus of Galeopithecus which was shown to possess a discoid placenta. Without entering into any further details, he figures (l. c., pl. 22) the said fœtus with outspread patagium and severed umbilical cord (fig. 1), and the same folded together in its intra-uterine position and attached by a thick and short umbilical cord to a disk-shaped placenta on which a number of radiating blood-vessels are indicated.

Gervais's figure corresponds in a general way with fig. 29 of this paper, only it is much smaller, and was probably not figured natural size. In our fig. 29 the circular placentary area is seen to lie as nearly as possible in the level of the uterine surface, and not to form such a marked button-shaped prominence as, for example, the placenta of Tarsius figured close to it (fig. 20) does to such a considerable extent.

Though both discoid, these two placentas are, no doubt, also in other respects profoundly divergent from each other. Although I have as yet only a provisional acquaintance with the chief stages of the placentation of Galeopithecus, I can more especially call the attention to the peculiar aspect of the placenta in figs. 24, 25, and 27.

It is already a discoid formation, but in these younger stages it is less compact and less intimately soldered with the uterine walls; the placental vessels, on the contrary, being mutually interwoven in an intricate manner, and being applied as a

[1] "Mémoire sur les formes cérébrales propres à différents groupes de mammifères," 'Journal de Zoologie,' vol. i, 1872.

delicate but prominent web (figs. 24 and 25) against the inner uterine surface.

The fœtus is connected with it by means of a short umbilical cord. Besides, there is a vascular connection between the fœtus and the remains of the yolk-sac.

The latter is represented in figs. 26—28, whereas in fig. 24 it has been dissected away in order to show the embryo enclosed by the amnion in its attachment to the placentary region.

In fig. 26 nothing has been removed but the uterine wall. The blood-vessels radiating over the yolk-sac are as distinctly visible as a spirit specimen will admit of. To the right as well as to the left the cut lumina of blood-vessels (cf. figs. 10 and 11) are seen to take their course in the thickness of the uterine wall.

On the right the placenta is represented by one free border, which is, moreover, loosened from any uterine attachment; the rest of the placenta is hidden from view by the embryo and its envelopes.

In the next figure (fig. 27), which has reference to this same specimen, the embryonic sheaths have been opened and the embryo is removed. The membranes to the right are the yolk-sac and the amnion. At the bottom of the uterine cavity the placenta can be distinguished.

In fig. 28 the embryo with its envelopes and with the placenta has been wholly scaled out of the uterus. Of the placenta an indented border is seen to the left of the figure, whereas to the right only the yolk-sac has been dissected and turned over; the amnion, however, is still in its place, and hides the embryo from view.

We have now to say a few words concerning the outer aspect of the uterus before and during pregnancy. More than in any of the species hitherto noticed the uterus of Galeopithecus may be said to be double, the vagina being spacious and thick-walled, and the two halves of the uterus (cf. figs. 2, 6 *a*, 7 *a*, 8 *a*, and 9 *a*) opening out into the vagina by separate openings. There is no unpaired median cavity in common between the two uteri, communicating by means of a single "os uteri" with

the vagina. Still when this proximal portion of the vagina is more closely examined, we find projecting into it a median prominence carrying a uterine crescentiform ostium on its left and on its right surface.

This fleshy projection must be looked upon as the partial soldering in the median plane of the distal parts of the two uteri, the fusion not having gone so far that it affects the uterine cavities.

Pregnancy soon reveals itself by swelling of one of the uteri (figs. 7—11). I have never noticed more than one fœtus at a time in Galeopithecus. The earlier swellings do not offer any peculiarity that could not be gathered from the figures 6—9; the later swellings, which come to take a marked ovoid shape, are externally characterised by an uncommon distension of vascular tracts in the uterine wall, which even in the preserved specimens stand out—in relief—against the flat outer uterine surface. This is no individual peculiarity, but is noticed in all the uteri of later stages. In fig. 11 the phenomenon is more marked than in figs. 10 *a* and 10 *b*; in all of them the central parts of this radiating vascular arrangement correspond with the mesometrium. The situation of the placenta is not in any special relation to this vascular arrangement. The way in which the ovary of Galeopithecus is partly hidden in a mesenterial fold (figs. 7 *b* and 8 *b*) has a certain resemblance to what was noticed above for Nycticebus and represented in fig. 4.

The fœtus of Galeopithecus that are figured on Pl. 12 (figs. 57, 58) show that the patagium is already indicated at an early moment. Fig. 58 represents, however, a not yet ripe fœtus; this is figured (natural size) in fig. 29.

After the young Galeopithecus is born it seems to remain attached to the mother's nipples for a not inconsiderable time, considering that on more than one occasion a pregnant uterus of the size of figs. 9—11 was prepared by one of my correspondents out of a female in which a young animal of the preceding litter was found clinging to the mother's breast.

Vernacular names for Galeopithecus in the Archipelago are

kubin or kubing, krendôh-kentjeng, and walang kêkkes (sometimes also applied to the flying squirrel or walang kôpo).

Tupaja. Figs. 12—17, 41, 59, 60.

This small Insectivore, which, as the vernacular name of Tupaj indicates, might easily be confounded with squirrels, was common in the plantations of coffee and cinchona in the Preanger districts. It often goes by the name of coffee rat, kekkès being the name by which the inhabitants of the above-mentioned districts generally designate it.

Tupaja has never more than two young at a time, as was noticed above. A uterus in an advanced stage of pregnancy is represented in fig. 17, the vaginal portion being here cut away. Most marked in this figure is the prominence of two reniform regions in the uterine wall. If the uterus were turned over, two exactly similar patches would be noticed. As in each of the two swellings only one embryo is contained, it follows that the placenta of Tupaja javanica must necessarily be double.[1] This is, in fact, the case, the two placentas lying right and left of the fœtus. They are connected with it (as fig. 41 distinctly proves) by an umbilical cord. This commences as a single strand of tissue, then bends upwards along the fœtus' side, and only divides into a quadruple set of blood-vessels above the fœtus' back. Two of these latter strands (each containing two vessels) continue in the same course, and vascularize the placenta which is situated on the side opposite to that where the umbilical cord passes upward, whereas the two other strands bend at an angle of 180° and vascularize the placenta that is on the same side as the umbilical cord. Fig. 41 will make all this clear; it was taken after one of the two swellings of the uterus was longitudinally cut open, the fœtus being also halved.

The perfect regularity in the situation of the two placentas of each fœtus is a phenomenon in which the maternal tissue plays a prominent part. If we examine transverse sections of very much earlier stages of pregnancy, such as are represented

[1] 'Proces Verbaal der Koninkl. Academie van Wetenschappen te Amsterdam,' 27 Mei, 1893.

in figs. 12—16, the lateral attachment of these early and much younger blastocysts is seen to have come about in the same spots where afterwards the reniform placenta will develop. The attachment of the early blastocyst, long before any allantois or allantoidean circulation has made its appearance, comes about by means of a very considerable proliferation of the trophoblast. The proliferating patches of trophoblast are double, and face the two spots in the uterine wall alluded to. It is beyond all doubt that even before this proliferation of the embryonic trophoblast has commenced the maternal tissue has become visibly modified in those four regions of the mucosa which correspond to the future placentary region, i. e. the right and left inner surface of the uterus-horn when cut transversely.

The tubular uterine glands are then more particularly limited to the mesometrical and antimesometrical regions of the lumen; on the spots in question the interglandular connective tissue has proliferated with partial displacement and partial obliteration of the glands there situated.

The uterine epithelium does not take part in this growth. It is, on the contrary, destroyed by the trophoblastic proliferation as soon as the blastocyst commences to adhere. This trophoblastic neoformation is then gradually vascularized (maternal blood penetrating into it), and undergoes a series of interesting but complicated histological transformations. In a future paper I propose to treat this placentation process of Tupaja more fully; it may here suffice to remark that against these early placentary cushions the yolk circulation is first applied, and that in further stages of pregnancy the yolk-sac is again removed from thence and replaced by the allantoidean blood-vessels which then constitute the definite double placenta.

The placentas are shed at birth as are those of Sorex and Erinaceus; they are not resorbed in situ as is that of Talpa.[1] The fully ripe placentas, shortly before birth, are in Tupaja connected with the maternal tissue by an area which all along its outer circumference is most easily detached and very loosely connected. Towards the centre, where the principal blood-

[1] Cf. 'Quart. Journ. Micr. Sci.,' vol. xxx, p. 346.

vessels pass in and out of the placentary structure, the adhesion is more firm.

Fœtus of Tupaja at a comparatively late stage of pregnancy are represented in their normal situation in their envelopes and in the uterine horn in figs. 59 and 60. These two were obtained from one and the same uterus. They measure (exclusive of tail) about 27 mm. At birth the fœtus has grown to a length of about 40—50 mm.

Manis. Figs. 42—45.

This genus, of which I have an extensive collection of uteri that were obtained from Manis javanica (the trengiling or tangiling of the natives), has of late years been investigated with respect to its placentation by Max Weber.[1] This fact enables me to restrict myself to a very short notice, the more so as the earliest stages, of which Weber makes no mention, have not yet been studied by myself at all, although they are also well represented in my collection. This, again, has to be reserved for a future publication. In explanation of the figures given on Pl. 12 I may say that fig. 42, which is enlarged twice, was an embryo that had been contained in the uterus of which a portion of the inner surface is represented in fig. 43. This inner surface is characterised by irregular villiferous bands, which become more numerous and more closely approximated as pregnancy advances.

The fœtus and its envelopes is very loosely applied against the maternal surface, outgrowths on the outer layers corresponding to and interlocking with the maternal villiferous bands just noticed.

Sections of these arrangements are figured by Weber.

In the uterus of fig. 43 the embryo of fig. 42 was enclosed in the membranes that are represented in fig. 44. These membranes are peculiar in so far as only a part of the sac appears expanded, a considerable part being more collapsed. Only the expanded portion carries villous bands that interlock with those

[1] 'Zoologische Ergebnisse einer Reise nach Niederländisch Ost-Indien,' vol. ii, 1891, pp. 1—118, pls. i—ix.

on the uterine surface. The pregnant horn of Manis carries but one embryo at a time, as was noticed by Weber. For the external shape of the uterus and the very considerable size of the ovaries I may also refer to that publication.

That the aspect of the fœtal envelopes is not always that of fig. 44 is shown in fig. 45, which represents a stage of about the same age but of a symmetrical development. The spacious yolk-sac is situated, as was already noticed by Weber, against the lower concavity of this sac. The fœtus enclosed in these envelopes will measure about 20 mm. in length from the vertex to the root of the tail; towards parturition it will have increased to the size of about 14 cm. from the centre of the skull to the root of the tail.

Additional Considerations.

Having terminated the description of the Spolia nemoris as at this moment they lie before me, I may be allowed to give a summary review of a couple of biological questions in their present stage towards the solution of which I hope in the first place to utilize the material collected.

These questions were already mentioned in the introduction, and have reference to—

I. The origin and morphological significance of the cell layers constituting the two-layered blastocyst of mammals.

II. The origin, the minute anatomy, and the morphological significance of the placenta.

I.

Since the very youngest mammalian blastocyst has been studied by means of sections and with the aid of the improved methods of the last decades, our knowledge of those incipient stages has grown very rapidly. For these earliest contributions we are indebted to Rauber,[1] van Beneden,[2] Lieberkühn,[3]

[1] "Die erste Entwickelung des Kaninchens," 'Sitzungsberichte der Leipziger Naturforschenden Gesellschaft,' 1875, p. 103.

[2] 'Bulletin de l'Acad. de Belgique,' t. 60, 1875, p. 686; five years later followed by "La formation des feuillets chez le lapin," 'Archives de Biologie,' vol. i, 1880.

[3] "Ueber die Kleimblätter der Säugethiere," 'Gratulationsschrift Nasse,' Marburg, 1879.

and Hensen.[1] The rabbit and the bat were more especially employed in these researches; Heape has added the mole, Selenka several other rodents as well as the opossum, whereas the hedgehog and the shrew were studied by myself. Of late Duval and also Robinson have again investigated the rat and the mouse. Nevertheless, we are at present very far from a consensus of opinion as to the significance and the genesis of the parts in the early didermic mammalian blastocyst.

In his well-known paper on the early development of the rabbit, Ed. van Beneden was one of the first to give a complete set of valuable illustrations of the segmentation of the mammalian ovum and of the consecutive stages between that process and the didermic blastocyst in which the mesoblast begins to make its first appearance.

Several of his figures have since passed into every text-book, although his interpretation, both of the earliest and of the later stages, is not adhered to in the form in which it was originally given. Concerning the earlier stages, Lieberkühn (l. c.) and afterwards Kölliker[2] have demonstrated that not only the lower layers, but also the epiblast of the embryo arises out of the inner cell-mass—v. Beneden's "masse endodermique." Concerning the later stages, they pointed out that van Beneden mistook (l. c., pl. 5, fig. 7, and pl. 7, fig. 2) for the mesoblast what is in reality the embryonic epiblast. The latter mistake was due to the presence of a trophoblastic layer of flattened cells outside that embryonic epiblast.

As to the development of the hypoblast, van Beneden made out that both in the rabbit and the bat it gradually extends centrifugally around the inner surface of the monodermic blastocyst, the centre of this irradiation being the thicker knob of tissue where the embryo is being shaped.

Similar formation of the hypoblast has been described by

[1] "Beobachtungen über die Befruchtung und Entwickelung der Kaninchen und Meerschweinchen," 'Archiv f. Anatomie und Entwickelungsgeschichte,' Bd. i, 1876.

[2] "Die Entwickelung der Keimblätter des Kaninchens," 'Zoolog. Anzeiger,' iii, 1880, pp. 370 and 390.

v. Beneden and Julin for the bat, by Heape for the mole, by myself for the shrew, and by Selenka for the opossum.

The extension of the hypoblast against the outer wall of the blastocyst is obtained in a different way in the hedgehog, as I have elsewhere described.[1] Instead of having to spread out against the inner surface of the wall of the blastocyst, the hypoblast of the hedgehog is from the beginning a solid knob which develops into a closed sac by distension. Further distension goes parallel to further growth of the didermic blastocyst.

The cause of the difference in development of the hypoblast is most probably the ever so much smaller size of the hedgehog's blastocyst when compared in corresponding phases with that of the rabbit, mole, &c. This is in its turn caused by the fact that the hedgehog's blastocyst, instead of being located in the uterine lumen, becomes included at a very early stage in the midst of maternal proliferating tissue. ('Anat. Anz.,' iii, p. 906.)

In 1892 Dr. Arthur Robinson[2] published a paper in which, starting from what he finds in the mouse and the rat, which he has studied for himself, he looks upon the process of hypoblast formation in the rabbit and bat in quite a different light than has been done by former investigators. The process in the hedgehog is, according to his views, more directly comparable to what he finds in the mouse. He has based on his observations a series of far-reaching theoretical speculations that partly correspond to views propounded by Sedgwick Minot in 1885.[3] Robinson concludes that in mammals it is not the hypoblast that spreads against the inner surface of the epiblastic wall of the blastocyst; but that, on the contrary, the epiblast, at a quicker or slower rate, spreads over the outer surface of a hypoblastic vesicle, which, according to

[1] 'Anat. Anzeiger,' Bd. iii, pp. 511, 906; and 'Quart. Journ. Micr. Sci.,' vol. xxx, p. 291.

[2] 'Quart. Journ. Micr. Sci.,' vol. xxxiii, p. 369.

[3] 'Buck's Reference Handbook of Med. Sciences,' i, 528, 1885; and 'American Naturalist,' September, 1889; also 'Human Embryology,' 1893, p. 107.

his views, is there from the very first and forms the greater part of the wall of the monodermic blastocyst.

In support of these views the author discusses the existing figures and descriptions of early mammalian blastocysts with considerable ingenuity. A couple of very difficult cases, which I see no possibility of including in Robinson's speculative attempt, are, however, by him passed over in silence. As such I would, for instance, point out Selenka's fig. 2, pl. 18, of the opossum ('Studien z. Entwickelungsgesch. der Thiere,' Heft 4), as compared both to earlier and later stages.

On p. 46 of Merkel and Bonnet's 'Ergebnisse der Anatomie und Entwickelungsgeschichte' (vol. ii, 1892), G. Born, in referring to Robinson's paper, recognises that if the views therein contained were confirmed, this would mean a total revolution of our present interpretation of the earlier stages of mammalian ontogeny. Born adds, "an der nothwendigen Nachprüfung der Resultate wird es nicht fehlen."

Such a "Nachprüfung" can be fully instituted with the aid of the material now in my possession. Already have I examined continuous section series through more than sixty segmentation stages and mono- and didermic blastocysts of Tupaja that had not yet adhered to the uterine wall, and through fourteen preparations of the same early stages of Tarsius.

I will elsewhere fully report about these preparations, but may be allowed now already to assert that they go dead against Dr. Robinson's speculations, and that I have no doubt that certain peculiarities observed in Tupaja will convince even Dr. Robinson of the fact that the outer layer of the mammalian monodermic blastocyst (i. e. the trophoblast) is not in direct continuity with the hypoblast cells inside of it.

On the other hand, we must recognize in Dr. Robinson's speculations, as also in the preceding attempt of Minot (l. c.) and Keibel ('Anat. Anzeiger,' vol. ii, p. 770),[1] laudable efforts

[1] I cannot admit with Keibel the possibility of a "Wachsthumsenergie derjenigen Zellen des Eies welche früher den Dotter umwuchsen," which would be unchecked for millions of generations after the disappearance of the yolk, and which is by him meant to explain certain formative processes in the blastocyst.

to the solution of a puzzle which the comparison of the holoblastic ova of Mammalia and of the lower Vertebrates and of Amphioxus present to us as yet. For my own part I hold that the principal reason why so many divergent and conflicting views have been consecutively adhered to with respect to the early mammalian blastocyst is this, that the appearance of a cavity in a segmenting ovum has never left room for a doubt whether this cavity could be anything else than a segmentation cavity which, as such, was proclaimed to be homologous with that of Amphioxus. This homology, I hold, does not exist. It should be remarked that both epiblast and hypoblast, that will build up the embryo, are in the early monodermic stages of the mammals contained inside this cavity; and that we have to expect the real segmentation cavity to arise between epiblast and hypoblast, as also in mammals it actually does later on.

If the space enclosed in the earlier monodermic stages is not the segmentation cavity, then there will be no more a priori difficulties to understand that a great portion of it is afterwards converted into the archenteron. In fact, as little difficulty as that a part of the cubic space inside the shell of a hen's egg becomes converted into the chicken's cerebral ventricles.

A comparison with another point in the embryology of the higher Vertebrates will show that the above conclusion about the cavity of the monodermic mammalian blastocyst is less hazarded than might appear at first sight.

Suppose for a moment that the details of the development of the amniotic Vertebrates were absolutely unknown to us, and that we were only fully acquainted with that of the anamnia.

And suppose then some embryologist to teach that the difference between the development of these anamnia and the as yet unknown higher Vertebrates would, for instance, prove to be this, that the latter manage to become suspended for a time in their own body-cavity, he would be in some danger of provoking hilarity, if not worse.

Still we find no difficulty in interpreting the latter phenomenon, thanks to the gradual steps by which embryology has

advanced. The segmenting ovum of mammals may thus be said to present the peculiarity, that among the products of the holoblastic segmentation only one or very few cells represent the real embryo; whereas a very considerable number that rapidly expand into a vesicle (against the inner wall of which the hypoblast becomes applied later on, either in one way or another), are segregated at an uncommonly early period in order that they may help to bring about a satisfactory attachment between the blastocyst (which *sensu strictiori* is as yet enclosed in this early vesicle) and the mother.

Only when the inner cell-mass shows the first traces of differentiation between those elements that will become hypoblast and those that will become epiblast cells, is the stage reached that corresponds to the blastula of Amphioxus; only then there can be question to look for the homologue of the segmentation cavity. As hypoblast and epiblast are at first firmly pressed together, this segmentation cavity is even then not yet present. The monodermic mammalian blastocyst is thus a *pseudo*-blastula stage, its cavity is not the real segmentation cavity, but a cavity which could not fail to arise ever since, for purposes of attachment and nutrition, an extreme case of precocious segregation of certain epiblast cells has come to occur in the mammalian ontogeny. These cells arrange themselves into a vesicle even before the two primary germinal layers of the embryo have differentiated.

There can be no doubt, however, that, phylogenetically, it is the epiblast from which these cells have been segregated; and this explains the intimate fusion which, after a certain time, obtains between this outer layer and the embryonic epiblast at the periphery of the latter.

If I am right in upholding that the cavity inside the monodermic mammalian blastocyst is not the segmentation cavity, and that this blastocyst is only a pseudo-blastula, then we must similarly conclude that it is *not a real holoblastic segmentation* which the mammalian ovum undergoes. Even the name of *tertiary holoblastic*, which Rabl proposes to apply to the mammalian ovum ("Theorie des Mesoderms,"

'Morph. Jahrb.,' vol. 15, p. 165), does not yet sufficiently express the fundamental difference by which the mammalian segmentation process is characterised.

There is no shred of evidence that with the disappearance of the yolk, which took place at a comparatively late stage when the mammalian character had already become predominant, the process of segmentation immediately fell back into the lines of the so infinitely more distant alecithal ancestral forms.

A further reason for the distrust with which we may look at this apparently holoblastic segmentation process is the fact that it finally results in the appearance of a tridermic blastocyst with elliptical blastoderm, primitive streak, &c., entirely corresponding to the arrangement of the Sauropsida. So these later stages have not returned to the earlier modes of development, but have continued along the lines laid down by the hereditary transmission of characters that were peculiar to those ancestral forms that possessed a considerable amount of food-yolk.

If the mammalian (pseudo) morula and (pseudo) blastula were indeed comparable with the same stages, *i. e.* with the true morula and true blastula in Amphioxus and the Amphibians, about one half of the segmentation spheres would represent potential epiblast, and the other half potential hypoblast. Now this is evidently not the case. By far the greater portion of these segmentation spheres gives rise to what will afterwards be not any integral portion of the embryo, but a part of the fœtal envelopes and of the membranous expansion by which the embryo is connected with the mother. Suppose we were able to repeat Roux's or Chabry's most important experiments on the partial destruction of one or more of the segmentation spheres with the earliest mammalian stages, then we might predict with great certainty from the data that Rauber, van Beneden, Heape, Selenka, and others have brought to light that only if the mother-cell of the inner cell-mass were attained, the normal development would be interfered with; and that in the case of other segmentation cells being punctured, only a local defect in the fœtal membranes would ensue. This hypothetical

experiment may still further drive home what is meant by the non-homology of the two cases of holoblastic segmentation and of the cavities which arise in these two cases inside the monodermic vesicles.

New and valid reasons are thus accumulated for designating the outer layer of precociously segregated epiblast-cells that form the wall of this vesicle by a separate name, which at the same time gives expression to the consideration that adaptation to nutritive conditions of an entirely novel nature has initiated this phenomenon of precocious segregation, simultaneously with the diminution and the final disappearance of food-yolk, a phenomenon that was consequent upon the passage from the Hypotherian to the Eutherian stage.

Already in 1888[1] have I proposed—and several embryologists, Dr. Robinson included, have since accepted—the name of trophoblast for this outer layer of the mammalian blastocyst.

Only lately[2] I have given a fuller definition of the term, which is, however, only in one respect an amplification of the original definition of 1888. Then already ('Anat. Anz.,' iii, 510), I remarked that to the trophoblast belonged all those peculiar cellular structures of the mammalian blastocyst which had been indicated by different authors as Reichert's cells and Rauber's "Deckschicht" (Kölliker), as "Träger" (Selenka), Ektodermawulst (Kölliker), horseshoe-shaped proliferation (van Beneden). To this list may yet be added Duval's "formation ectoplacentaire."

The amplification of 1893 just alluded to was this, that I not only defined the trophoblast as "the epiblast of the mammalian blastocyst that does not take part in the formation of the embryo," but that I added to this, "or of the inner lining of the amnion cavity."

The difference which obtains between the trophoblast and between the embryonic epiblast contributing to the formation of the embryo and of that inner lining of the amnion cavity, is

[1] 'Anatomischer Anzeiger,' July, 1888, p. 510.

[2] 'Proces-verb. van de Kon. Akad. van Wetenschappen te Amsterdam,' 27 Mei, 1893.

most distinctly brought out in such mammals as Pteropus, Cavia, Tupaja, and others. Take, for instance, Selenka's figure of the guinea-pig's blastocyst,[1] Göhring's of that of Pteropus.[2] In these latter figures, we see the epiblastic knob which is enclosed between the trophoblast and the hypoblast of the didermic blastocyst, hollowing out into a cell-mass, of which the upper surface thins out and becomes the epiblastic clothing of the amnion cavity, whereas the lower surface thickens and becomes the epiblast of the blastodermic surface out of which the embryo will be modelled.

I have no doubt that in the cases of Erinaceus and Sorex a similar sharp line of demarcation may be drawn between the epiblast that will develop into the lining of the amnion and between the trophoblast, although here this distinction is not so self-evident as in the preceding cases. And I suspect that even such cases as that of the rabbit will some day admit of a sharper delimitation of these two.

But even where such a sharp delimitation is not as yet always possible in the later stages of the blastocyst, the earlier stages are all the more evident.

The Ornithodelphia are not as yet affected by the causes which determine the differentiation of a special trophoblast in the higher placental Mammalia. In the Didelphia we may hope to find certain transitory stages. Thus the early stages of Phascolarctos, the ovum of which has been described by Caldwell, may be expected to be especially instructive. Already in the opossum Selenka has described the very peculiar proliferation in the outer layer of the early blastocyst (l. c., Heft 4, pl. 20, figs. 2, 5, and), which is no doubt precursory to the ever so much more important proliferations of the trophoblast which occur in most of the higher orders of mammals.

In this paper it has already been noticed how both in Tupaja and in Tarsius, portions of the trophoblast undergo

[1] 'Studien zur Entwickelungsgesch. der Thiere,' Heft 3, pl. 12, figs. 13—15, 73.

[2] Ibid., Heft 5, pl. 41, figs. A—C, 1; 2, 4, and 6.

very active proliferating processes preparatory to the placentary fixation of the blastocyst, whereas in my former papers I have described the same activity for Erinaceus[1] and Sorex.[2]

Robinson's speculations having tended to bring the part that the hypoblast plays in the mammalian blastocyst more into prominence, E. van Beneden has, on the contrary, upheld[3] that the inner layer—his "so-called" hypoblast—of the mammalian blastocyst is not homologous with the hypoblast of Amphioxus, but should be regarded as a yolk-envelope and be no longer designated by the name of hypoblast, but by that of lecithophore.

These views, tentatively accepted by Rabl,[4] have been combated by Keibel,[5] by myself,[6] and by others. Also with respect to this question I have no doubt that the material here described will furnish very useful and perhaps decisive data. Decisive, for example, with respect to the question whether mesoblast takes its origin out of this hypoblast layer (v. Beneden's lecitophore), as Bonnet[7] and Hubrecht[6] have distinctly stated and figured it to do, although others (Keibel,[8] for instance) deny this. It is clear that such participation in the formation of the mesoblast is in itself sufficient to invalidate v. Beneden's considerations about the "lecitophore" and to establish the homology of this layer with the hypoblast of Amphioxus and the lower Vertebrates.

I have myself tried to explain the peculiarities that in mammals also attend the formation of the hypoblast by the sugges-

[1] 'Quart. Journ. Micr. Sci.,' vol. xxx.

[2] Ibid., vol. xxxi.

[3] 'Anatomischer Anzeiger,' iii, p. 713.

[4] "Theorie des Mesoderms," 'Morphol. Jahrb.,' Bd. xv.

[5] "Zur Entwickelungsgesch. der Chorda bei den Säugern," 'Archiv für Anat. und Physiol. Anat.,' Abth., 1889.

[6] "Development of the Germinal Layers of Sorex vulgaris," 'Quart. Journ. Micr. Sci.,' vol. xxxi, 1890.

[7] "Beiträge z. Embryologie d. Wiederkäuer," 1 und 2, 'Archiv für Anat. und Physiol.,' Anat. Abth., 1884, p. 170, and 1889.

[8] "Ueber die Entwickelungsgesch. des Schweines," 'Anat. Anz.,' vi, 1891, and Schwalbe's 'Morph. Arbeiten,' Bd. iii, 1893, S. 69.

tion that precocious segregation of part of the hypoblast comes into play and that we have to distinguish a cœnogenetic and a palingenetic hypoblast. This suggestion has been favorably received; the natural counterpart of it is the above sketched precocious segregation of part of the epiblast. Both are adaptations to similar external conditions.

II.

The origin, the minute anatomy, and the morphological significance of the placenta have been of late inquired into by a considerable number of independent investigators. It may suffice to cite among the more recent ones Duval,[1] Strahl,[2] Frommel,[3] Fleischmann,[4] van Beneden,[5] Masius,[6] Lüsebrink,[7] Heinricius,[8] Minot,[9] Hubrecht,[10] and others. Questions that were more particularly entered into are those that concern the fate of the maternal epithelium at the spot where the blastocyst comes to adhere against the uterine surface. In Erinaceus it undergoes changes that are very different from those that take place with it in the rabbit, and different again from what happens with it in the Carnivora. In Sorex the fate of the

[1] M. Duval, "Le Placenta des Rongeurs,' Paris, 1889–93.

[2] H. Strahl, "Untersuchungen über den Bau der Placenta," I—IV, 'Arch. f. Anat. u. Physiol.,' 1889, 1890. V. Anat. Hefte von Merkel u. Bonnet, 1892.

[3] R. Frommel, 'Ueber die Entwickelung der Placenta bei Myotus murinus,' Wiesbaden, 1888.

[4] A. Fleischmann, 'Embryologische Untersuchungen,' Hefte 1—3, Wiesbaden, 1889–93.

[5] E. v. Beneden, "De la formation et de la constitution du placenta chez le Murin," 'Bull. Acad. roy. Belg.,' 3e ser., t. 15, 1888.

[6] J. Masius, "De la genèse du placenta chez le lapin," 'Archives de Biologie,' vol. ix, 1889.

[7] F. W. Lüsebrink, "Die erste Entwickelung der Zotten in der Hundeplacenta," Anat. Hefte von Merkel u. Bonnet, ii, 1892.

[8] Heinricius, "Ueber die Entw. u. Struct. d. Placenta beim Hunde," ibid. "bei der Katze," 'Arch. f. mikr. Anat.,' Bde. 33 u. 37.

[9] C. S. Minot, "Uterus and Embryo," 'Journal of Morphology,' ii, 1889.

[10] Hubrecht, "Erinaceus," 'Quart. Journ. Micr. Sci.,' xxx, 1889; "Sorex," ibid., xxxv, 1894; and 'Verhandel. k. Akad. v. Wetensch. Amsterdam,' 2e Sec., vol. iii, 1893.

maternal epithelium is yet more peculiar, considering the fact that an uncommonly marked proliferation of this epithelium precedes its definite disappearance.

Secondly, the question has been much ventilated which part the trophoblast plays in the attachment of the blastocyst. Both in Insectivora (Erinaceus, Sorex, by myself) and in Rodentia (rabbit, mouse, rat, Meriones, Cavia, by Duval) this has been fully inquired into, and overwhelming evidence has been forthcoming to show that this epiblastic layer and no other but this layer contributes in an unexpected measure to the genesis of the tissues that constitute the placenta.

It may even be said that since the penetration of maternal blood into lacunar spaces of the hedgehog's trophoblast that are devoid of any vascular endothelium has been described as occurring even at stages as early as the didermic blastocyst,[1] and since Duval made his first communication about the rabbit and other Rodents to the Paris Société de Biologie,[2]—communications that have soon after been worked out in his masterly volume, 'Le Placenta des Rongeurs' (Paris, 1889–92),—a conflict of opinion has arisen about the real nature of the placenta, in which on one side are a majority of the above-cited German anatomists, and on the other the two authors just named and also E. van Beneden with reference to the bat ('Comptes Rendus de la Société de Biol.,' vol. v, Novembre, 1888), and J. Masius, his pupil, with reference to the rabbit (l. c.).

The question centres in the way in which the osmotic interchange between the maternal and the embryonic blood comes about, influenced as it is by preparatory processes that take place in those regions where the trophoblast of the blastocyst comes in contact with the inner lining of the uterus.

Now this phenomenon is easy enough to understand in the horse, the pig, and several other mammals on which the

[1] Hubrecht, 'Kleimblätterbildung und Placentation des Igels," 'Verhandlungen der Anat. Gesellsch.; Versammlung zu Würzburg,' Mai, 1888; 'Anat. Anz.,' iii, p. 512; and "The Placentation of *Erinaceus europæus*," 'Quart. Journ. Micr. Sci.,' vol. xxx.

[2] 'Comptes-rendus de la Société de Biologie,' Mars et Juillet, 1887; Octobre et Novembre, 1888, vols. iv et v.

researches of Turner, Ercolani, &c., have already years ago thrown a flood of light.

We find there what we find repeated in two of the genera which are treated of in this paper, viz. Manis and Nycticebus. The outer layer of the blastocyst acquires numerous villiferous processes that are vascularized and fit into vascular crypts of the maternal wall, out of which they are retracted at birth with the greatest facility. In Nycticebus the two epithelia, both the embryonic and the maternal, remain intact, and the osmotic interchange takes place through two cell-layers of different origin and of different physiological significance (phylogenetically).

As soon as the complications in this arrangement commence to make themselves felt, which are so varied and so characteristic in the different and so-called "deciduate" orders of mammals, a clear insight is much less easily obtained. Partly because as yet only a restricted number of genera has been examined sufficiently in detail; partly because when such investigation has taken place the different observers do not always concur in the interpretation of the phenomena which present themselves on examining the microscopical preparations of the same species.

A significant cell-layer is by the one declared to be maternal, by the other to be of embryonic origin. Maternal blood is by the one said to be enclosed in vascular spaces, that never lose their real character of further extensions of capillary vessels, whereas the other pretends that the maternal blood penetrates sometimes at a very early, sometimes at a later stage of the ontogenesis into lacunar spaces that are wholly surrounded by tissue that is exclusively of embryonic origin.

Duval very tersely expresses the latter view, of which he is himself one of the staunchest advocates, as follows:—"Le placenta représente à son origine, une hémorragie maternelle, circonscrite ou enkystée par des éléments fœtaux ectodermiques." The fact that certain interpretations based on older researches, that could not yet profit by the modern technical improvements, have been adopted in the text-books,

gives a long vitality to views which would most probably be soon abandoned if the problem were now-a-days brought forward for the very first time. Similarly, generalisations that were based on incomplete data, although fully justified at the time when they were made, are now found to obstruct the way to a certain extent.

One of the mammals that will facilitate the real understanding of the method according to which the very simple manner of fœtal interchanges above alluded to has been converted into the more complicated placentary structures, is the mole. Some years ago I called attention to the fact ('Quart. Journ. Microsc. Science,' vol. xxx, pp. 346 and 388) that here, too, embryonic villi that cover the fœtal envelopes are easily drawn out of their sheaths at birth, and that no afterbirth is shed, although the animal has a discoid placenta, which up to lately was held to mean that it was also deciduate. I then expressed the opinion that not only the mole is not deciduate, but that even embryonic tissue is left behind against the uterine surface, and is gradually resorbed in situ.

According to the patient investigations made by Mr. Vernhout, a pupil of the Utrecht Zoological Laboratory, which are at present in the press, this is actually the case. Mr. Vernhout has cleared up the early details of the mole's placentation, and comes to very different conclusions from those of Strahl.

We may say that in the mole the epithelial connection, as it was described above for Nycticebus and others, is a phase that is very rapidly passed over, and that it is followed by the application of a trophoblastic cell-layer against the maternal epithelial layer. According to Mr. Vernhout's investigations, based upon preparations which I have myself repeatedly had occasion to compare with the drawings which he is about to publish, the maternal epithelium is very rapidly destroyed, the trophoblast now becoming a pseudo-epithelium by which the denudated mucosa and its deepening crypts are covered. Into these crypts, which are in fact of embryonic origin, the allantoic villi penetrate and are withdrawn out of them at birth, the trophoblastic pseudo-epithelium, and the further derivates it

has given origin to, remaining in connection with the maternal tissues.

I hold this to be not a secondary modification which has arisen among mammals that were already frankly deciduate, but, on the contrary, a more primitive developmental phase. In very many cases it may have preceded that more complete arrangement in which the uterus, after having expelled the fœtus, also rids itself (be it even at the cost of some of its own elements—rapidly renovated after parturition) of the growths (afterbirth) by which the embryo has succeeded to obtain so firm a hold on the maternal sanguiniferous tissues.

If we look at the Carnivora, at the bats, the rodents, the Primates, and the Insectivora, we find their more complicated placentary structures to belong to very divergent types. In the latter order there is no common type, but a different one for nearly every genus. The shrew, the mole, the hedgehog, and the Tupaja are all most incredibly divergent with respect to their placentary arrangements. Only when the comparative investigations shall have covered a more considerable number of different genera, the time for new theoretical generalisations will have arrived.

Towards the accumulation of material that would be thus available I hope the Spolia Nemoris here described may contribute.

EXPLANATION OF PLATES 9, 10, 11, & 12,

Illustrating Professor A. A. W. Hubrecht's paper, "Spolia Nemoris."

ov. Ovary. *lig.* Uterine ligament. *M.* Muscularis of the uterine wall. *m.* Mucosa of the uterine wall. *R.* Hollow recesses clothed with epithelium in the chorion of Nycticebus. *ap.* Apertures by which these open to the exterior. *amn.* Amnion. *u.* Umbilical cord. *V.* Chorionic villi of Nycticebus. *cr.* Crypts clothed with epithelium, in which these villi fit. *gl.* Uterine glands.

PLATE 9.

All figures natural size.

FIG. 1.—Tarsius spectrum. A pregnant uterus in the latest stages. In Fig. 1 the barren horn of the uterus, with coiled oviduct and ovary, are yet visible on the top of the swelling that contains the fœtus. The other ovary protrudes in the left lower border of the figure. At the right lower border the uterine wall shows a rupture ; here the vagina formed its continuation.

Utr. Mus. Cat. n°· Tarsius 10.

FIG. 2.—Tarsius spectrum. Earlier phase of pregnancy. One ovary (*ov.*) visibly more considerably swollen than the other.

Utr. Mus. Cat. n°· Tarsius 11.

FIGS. 3—5.—Three uteri of Nycticebus tardigradus. Figs. 3 and 5 front views. Fig. 4 viewed from above to show the peculiar shape of the uterine horns. In the latter figure the vagina and the two ligamenta rotunda are bent forwards from under the horns. Ovaries partly hidden from view by fold, including oviduct. Fig. 5 is the stage furthest advanced ; the fully ripe fœtus reaches up to four times this size.

Fig. 3.—Utr. Mus. Cat. n°· Nycticebus 6.
Fig. 4.— „ „ „ 7.
Fig. 5.— „ „ „ 56.

FIGS. 6*a* and 6*b*.—Galeopithecus variegatus. The double uterus in a very early stage of pregnancy. 6*a* seen from behind, 6*b* seen from above. The two halves of the uterus open out into the vagina by separate canals and openings. There is no median portion in common.

Utr. Mus. Cat. n°· Galeopithecus 3.

FIGS. 7*a* and 7*b*.—The same, in a somewhat later stage of pregnancy.

Utr. Mus. Cat. n°· Galeopithecus 13.

Figs. 8*a* and 8*b*.—The same, with one of the uteri already very markedly swollen.

Utr. Mus. Cat, n$^{o.}$ Galeopithecus 27.

Figs. 9*a* and 9*b*.—The same, in a later stage.

Utr. Mus. Cat. n$^{o.}$ Galeopithecus 18.

Figs. 10*a* and 10*b*.—The same, with the indication of very much widened blood-vessels in the uterine wall. 10*a* seen sideways, 10*b* seen from below.

Utr. Mus. Cat. n$^{o.}$ Galeopithecus 16.

Fig. 11.—Side view of a pregnant uterus of Galeopithecus, at nearly full term; the blood-vessels in the uterine wall yet more prominent.

Utr. Mus. Cat. n$^{o.}$ Galeopithecus 14.

Figs. 12—16.—Five uteri in early stages of pregnancy of Tupaja javanica.

Utr. Mus. Cat. n$^{os.}$ Tupaja 251, 62, 254, 17, 39.

Fig. 17.—Pregnant uterus of Tupaja at full term, both halves containing a fœtus, the right placenta of the left fœtus and the left placenta of the right fœtus being visible as a reniform thickening in the uterine wall. The other placentas are situated quite symmetrically on the opposite side, invisible here.

Utr. Mus. Cat. n$^{o.}$ Tupaja 170.

PLATE 10.

All the figures (with the exception of Figs. 20, 24, and 25) natural size. Colour as shown by spirit specimens.

Fig. 18.—Tarsius spectrum. Fully developed fœtus folded together in fœtal membranes with discoid placenta, viewed from above, on the left side of the drawing. The placenta is actually attached to the maternal tissue only in the central angular spot.

Utr. Mus. Cat. n$^{o.}$ Tarsius 10.

Fig. 19.—The same, seen in profile to show the relative height of the placenta.

Fig. 20.—Tarsius spectrum. Part of the uterine wall after removal of the fœtus. Umbilical cord and placenta in situ. The latter cut longitudinally. Enlarged $\frac{2}{1}$.

Utr. Mus. Cat. n$^{o.}$ Tarsius 15.

Fig. 21.—The same, as seen from below before the placenta was cut in two.

Utr. Mus. Cat. n$^{o.}$ Tarsius 15.

Fig. 22.—Highly pregnant uterus of Nycticebus, with only the muscularis peeled off. Cf. Figs. 30–32, 52.

Utr. Mus. Cat. n$^{o.}$ Nycticebus 24.

Fig. 23.—Another pregnant uterus of Nycticebus, with three incisions in

the uterine wall. Two triangular flaps of muscularis and mucosa are folded backwards and reveal the fœtus enclosed in its villiferous envelope. Cf. Figs. 31, 32, 50, 51.

Utr. Mus. Cat. n°· Nycticebus 23.

Fig. 24.—Galeopithecus variegatus. Pregnant uterus, opened opposite to the placenta. Embryo in amnion. The yolk-sac has been removed, together with the portion of the uterine wall. Enlarged twice.

Utr. Mus. Cat. n°· Galeopithecus 18.

Fig. 25.—Placentary area of the same, enlarged three times, after removal of the embryo.

Utr. Mus. Cat. n°· Galeopithecus 18.

Fig. 26.—Another uterus of Galeopithecus, in which the wall opposite the placenta has also been removed, but in which the fœtal membranes, &c., are as yet all of them in situ. The blood-vessels on the yolk-sac are clearly visible. To the right of the figure the section of the uterine wall has passed through a portion of the placentary region.

Utr. Mus. Cat. n°· Galeopithecus 19.

Fig. 27.—The same stage as that of Fig. 26, after the fœtal envelopes have been opened and turned over (yolk-sac and amnion) to the right. The embryo is removed; the placenta is visible.

Utr. Mus. Cat. n°· Galeopithecus 19.

Fig. 28.—A similar stage, peeled out of the uterus. The placenta is partly visible on the left. The yolk-sac has been cut and turned over to the right, the embryo is yet enclosed by the amnion.

Utr. Mus. Cat. n°· Galeopithecus 1.

Fig. 29.—Uterus of Galeopithecus at full term, opened. The ripe fœtus is attached by the umbilical cord to the discoid placenta, which presents a smooth surface, continuous with that of the uterine wall in which it is implanted.

Utr. Mus. Cat. n°· Galeopithecus 17.

PLATE 11.

Figs. 30—33, 35, 36, and 41, natural size. Figs. 34 × 3, 37 and 38 × 27, 39 and 40 × 16.

Fig. 30.—Nycticebus tardigradus. The same uterus as that of Fig. 22. The flaps of the muscularis in the same position; mucosa opened; villiferous chorion inside this opened likewise; amnion partially removed.

Utr. Mus. Cat. n°· Nycticebus 24.

Fig. 31.—Uterus of Nycticebus in somewhat earlier stage of pregnancy, opened by a circular incision. Muscularis and reticular mucosa have here been left in their natural connection, and the portion of the uterine wall that is

here bent to the left has been removed from the subjacent villiferous chorion without any effort of traction.

Utr. Mus. Cat. n°· Nycticebus 84.

FIG. 32.—A similar stage of the same specimen, but in which not only the uterine wall but also the fœtal envelopes have been opened and have also been folded back. Embryo removed.

Utr. Mus. Cat. n°· Nycticebus 45.

FIG. 33.—A ring-shaped section of a Nycticebus uterus, nearly at full term. The embryo alone has been removed. The umbilical cord is seen to divide into a number of vasiferous strands, attached to the inner surface of the chorion. The fœtal envelopes (with the exception of the amnion, which has been removed with the fœtus) have been left in their natural position.

Utr. Mus. Cat. n°· Nycticebus 41.

FIG. 34.—The inner surface of the chorion enlarged three times, showing finely ramifying blood-vessels, both afferent and efferent, the two of different colour in the preserved specimens. Chorionic recesses (cf. Figs. 39 and 40) form conspicuous round projections inwards. The radiate spots correspond to the chorionic villi present on the opposite side.

Utr. Mus. Cat. n°· Nycticebus 41.

FIG. 35.—Nycticebus fœtus, wholly enveloped by the villiferous chorion, very shortly before birth. Between the villi the apertures (*ap.*) of the chorionic recesses (cf. Fig. 39) are visible to the naked eye. To the right the villi are larger, but also more flattened and wider apart.

Utr. Mus. Cat. n°· Nycticebus 34.

FIG. 36.—The same Nycticebus embryo of Fig. 30, to show its attachment by means of the umbilical cord (*u.*) to the chorionic envelope, which is partially turned inside out.

Utr. Mus. Cat. n°· Nycticebus 24.

FIGS. 37 and 37 *a.*—Three chorionic villi of Nycticebus as seen from above, enlarged × 27. They were taken from the specimen of Fig. 30, and are seen to be multilobulate.

Utr. Mus. Cat. n°· Nycticebus 24.

FIG. 38.—The prominent network of the mucosa in which the chorionic villi fit. Also taken from the same specimen and enlarged × 27.

Utr. Mus. Cat. n°· Nycticebus 24.

FIG. 39.—Transverse section of a portion of the chorion of Nycticebus. Blood-vessels are red. Epithelial covering of chorionic villi here and there thickened, more especially on the tops of the villi. Chorionic epithelium continuous in the round and flattened recesses (*R.*) that open out in the extra-chorionic space by the apertures (*ap.*).

Utr. Mus. Cat. n°· Nycticebus 24.

FIG. 40.—Another section of the chorion of Nycticebus, but with the

portion of the uterine wall against which the chorion is applied *in situ*. The numerous indentations and reticularly arranged spaces into which the chorionic villi fit are also covered by an epithelium which is generally somewhat flatter than that of the chorion. The maternal as well as the fœtal blood-vessels are indicated by a red colouring. It can here be seen that the separation which in Figs. 22 and 30 was brought about between muscularis and mucosa must have been facilitated by the intervening glandular region here indicated. The chorionic recess in this figure protrudes further inwards than those of Fig. 39.

Utr. Mus. Cat. n°· Nycticebus 45.

Fig. 41.—One of the two compartments of the pregnant uterus at full term of *Tupaja javanica* (cf. Fig. 17), opened by a longitudinal incision. The fœtus was cut in two by this operation, the one half that is figured in outline fitting in the uterine segment to which it remains attached. The vessels of the umbilical cord (which passes towards the dorsal side of the fœtus) are there seen to divide into four principal tracts, two for each placenta. The placenta which was situated to the right of the fœtus is figured in the lower, that which was situated to the left of it in the upper segment. The latter has thus to be placed *in situ* by revolving downwards around its base line by 180°. The cut vessels at the top of the figure will then be seen to become continuous with those at the bottom of it.

Utr. Mus. Cat. n°· Tupaja 258.

PLATE 12.

All the figures natural size with the exception of Figs. 42, 46, 55 and 56, which are enlarged twice.

Fig. 42.—Early embryo of *Manis javanica* prepared out of the fœtal envelopes that are represented in Fig. 44. Enlarged × 2.

Utr. Mus. Cat. n°· Manis 29.

Fig. 43.—View of the inner surface of a pregnant uterus of *Manis javanica* that contained the fœtus and fœtal envelopes of Figs. 42 and 44. Villosities on the inner uterine surface united into irregular bands.

Utr. Mus. Cat. n°· Manis 29.

Fig. 44.—Fœtal envelopes of *Manis javanica* that contained the fœtus which is represented (enlarged twice) in Fig. 42. These fœtal envelopes were obtained intact (after the uterus had been opened) by simply floating them out. The fœtus was contained in the left part. The twisted projection stretching to the right was devoid of villosities, and measures about twice the length of the villiferous portion in which the fœtus and yolk-sac were found. It is an example of an asymmetrical arrangement of the fœtal envelopes in contrast to those of Fig. 45.

Utr. Mus. Cat. n°· Manis 29.

Fig. 45.—Manis javanica. Embryo of about the same age in its fœtal envelopes, the latter more symmetrically developed than in Fig. 44. The streaks and bands on the surface corresponding to villous bands on the uterine wall are clearly visible. The yolk-sac is internally applied against the lower concave surface.

Utr. Mus. Cat. n°· Manis 71.

Fig. 46.—Tarsius spectrum. Young embryo removed out of its enveopes, seen in profile. Enlarged $\frac{2}{1}$.

Utr. Mus. Cat. n°· Tarsius 11.

Fig. 47.—Nearly ripe fœtus of Tarsius spectrum enclosed in all its membranes. The discoid placenta is here visible at the top. The only point of adhesion with the uterine wall is found in the midst of this placentary disc (cf. Figs. 18 and 19).

Utr. Mus. Cat. n°· Tarsius 10.

Fig. 48.—Fœtus of Tarsius of about the same age removed out of its fœtal membranes.

Utr. Mus. Cat. n°· Tarsius 15.

Fig. 49.—The fœtal membranes of a Tarsius at full term after the removal of the fœtus. Discoid placenta and umbilical cord distinct.

Utr. Mus. Cat. n°· Tarsius 101.

Fig. 50.—Fœtus of Nycticebus tardigradus enclosed in its villiferous chorion. Obtained by very gently turning upside down the opened uterus (Fig. 51) in which it was enclosed.

Utr. Mus. Cat. n°· Nycticebus 84.

Fig. 51.—One half the uterus of Nycticebus in which the fœtus of Fig. 50 has been enclosed. View of the inner surface.

Utr. Mus. Cat. n°· Nycticebus 84.

Fig. 52.—The mucosa of Nycticebus of the stage represented in Figs. 22 and 30, peeled off from the muscularis and seen from the inside.

Utr. Mus. Cat. n°· Nycticebus 24.

Fig. 53.—Nycticebus fœtus in all its envelopes, the latter being more folded than in Fig. 50.

Utr. Mus. Cat. n°· Nycticebus 23.

Fig. 54.—A later fœtus of Nycticebus prepared out of its envelopes, part of which are still in connection with the umbilical cord and visible above the head of the fœtus.

Utr. Mus. Cat. n°· Nycticebus 54.

Fig. 55.—The villiferous chorion in a very late stage of pregnancy. Enlarged × 2. To the right the villi are more flattened (cf. Fig. 35).

Utr. Mus. Cat. n°· Nycticebus 34.

Fig. 56.—The reticulated mucosa of a similar late stage of pregnancy. Enlarged × 2.

Utr. Mus. Cat. n°· Nycticebus 34.

Fig. 57.—Embryo of Galeopithecus removed from its envelopes, front view. The severed umbilical cord is seen protruding between the claws.

Utr. Mus. Cat. n°· Galeopithecus 54.

Fig. 58.—Much younger embryo of the same, viewed in profile.

Utr. Mus. Cat. n°· Galeopithecus 19.

Fig. 59.—Fœtus of Tupaja javanica in its half of the uterus. This latter was slit open longitudinally, and the left placenta visible. The right placenta is hidden from view by the embryo.

Utr. Mus. Cat. n°· Tupaja 302.

Fig. 60.—The same, the fœtus from the other half of the same uterus. The head of the fœtus is seen to be directed distally towards the vagina.

Utr. Mus. Cat. n°· Tupaja 302.

Studies on the Comparative Anatomy of Sponges.

VI. On the Anatomy and Relationships of Lelapia australis, a Living Representative of the Fossil Pharetrones.

By

Arthur Dendy, D.Sc.

With Plate 13.

I. Introductory Remarks.

In my memoir on the 'Structure and Classification of the Calcarea Heterocœla,' recently published in this Journal (1), I had occasion to refer to that very remarkable calcareous sponge Lelapia australis. Unfortunately this species is extremely rare, only two specimens being as yet known. Both of these were dredged by Mr. J. Bracebridge Wilson, M.A., off the Victorian coast, and both were sent to Mr. Carter, by whom their external characters and spiculation were described (without illustration) in the 'Annals and Magazine of Natural History' (2). At the time when I wrote I had never had the opportunity of personally investigating this sponge, but since then Mr. Carter, with his usual generosity, has most kindly sent me a portion of the better of the two specimens, preserved in spirit.[1] He has also sent me an unpublished sketch of the entire sponge, and has permitted me to make use of it in the present memoir (fig. 1). For this and many other kind-

[1] The specimen itself is in the British Museum.

nesses of a similar nature I desire to express my most sincere thanks to Mr. Carter. The material was fortunately in sufficiently good condition to enable me to make out the structure of the canal system, and to establish the correctness of my supposition that it belonged to the Leuconoid type. By far the most interesting feature of the species, however, proved to be the very remarkable reticulated fibrous character of the skeleton, which appears to have hitherto escaped observation. This character is unknown in any other living calcareous sponge, while it forms the most prominent feature in the great fossil group "Pharetrones" of Zittel (3), hitherto regarded as entirely extinct. Lelapia australis may therefore be looked upon as the only known living representative of this important group,[1] and a minute study of its anatomy thus acquires an exceptional interest.

I have much pleasure in again expressing my most sincere thanks to Professor G. B. Howes for kindly undertaking the correction of the proof sheets in my absence from England.

II. Anatomy of Lelapia australis.

A. External Form.

The larger of the two specimens (fig. 1) measured $3\frac{1}{4}$ inches in length by 1 inch in greatest diameter, and is thus described by Mr. Carter (2, p. 148):—"Cylindrical, clavate, the largest part upwards, somewhat curved or bent upon itself, rugose longitudinally. Consistence firm. Colour dark grey. Surface even, smooth, interrupted by the projection of crooked ridges extending from the free to the fixed end, subspirally and longitudinally, in broken lengths, sometimes reduced to mere scattered tubercular points, most pronounced on the concave side towards the mouth, least so on the opposite side: largest and most continuous ridge $\frac{1}{3}$ inch long, $\frac{1}{48}$ inch broad, and $\frac{3}{48}$ inch high. Pores plentifully scattered over the surface, not

[1] Whether the group, as it stands, is a natural one, appears to me doubtful.

remarkably large. Vent single, terminal, represented by a narrow elliptical opening about $\frac{1}{3}$ inch in its longest diameter, so constricted in the centre as to be closely approximated by an infolding of the lip on each side; provided with a peristome, whose spicules here are broken off short; leading into a cloaca corresponding in shape with the specimen, that is, wide above, narrowed to a point below (after which the stem becomes solid)."

The specimen thus described is obviously a single Leuconoid individual. The smaller specimen, however, as described by Mr. Carter, showed some indication of a tendency to branch, and possibly the species may sometimes form branching colonies.

B. The Skeleton. 1. The Spicules.

The following account of the spicules is taken from preparations boiled out with caustic potash, as it is extremely difficult to obtain a satisfactory view of entire spicules in their natural position. I have not had the opportunity of examining the spicules of the peristome, but we learn from Mr. Carter's writings that there is no important modification amongst these which is not also met with elsewhere. All three principal types of calcareous spicules are met with, but the quadriradiates are rare, and the apical ray is very feebly developed.

Oxeote Spicules.—Three varieties may be clearly distinguished:

(1) Large, stout, fusiform; usually slightly curved and slightly irregular in diameter; tapering gradually to a sharp point at each end (fig. 2, *a*). Size variable, when fully grown about 1·9 by 0·11 mm.

(2) Long, straight, and very slender, gradually and sharply pointed at both ends, and sometimes slightly hastate or bayonet-shaped (fig. 2, *b*). Size variable, say about 0·9 by 0·008 mm., but often less.

(3) The so-called "mortar-spicule." Minute; straight or slightly crooked; gradually and sharply pointed at both ends,

lanciform or hastate at one (fig. 2, *c*). Size variable, say about 0·08 by 0·004 mm.

Triradiate Spicules.—Here again three principal varieties may be clearly recognised :

(1) Normal sagittal triradiates ; with wide oral angle; with long straight shaft (or basal ray) and much shorter lateral (or oral) rays which may be straight or slightly curved away from one another (fig. 2, *e*). All rays rather slender, and gradually and sharply pointed ; orals measuring about 0·25 by 0·016 mm. ; basal about 0·46 by 0·016 mm. (The subgastral sagittal triradiates usually have somewhat longer and stouter rays.)

(2) Laterally extended sagittal triradiates; with oral rays so widely divergent as to be almost in the same straight line, and basal ray very much shorter, reduced almost to insignificance (fig. 2, *f*). Oral rays almost straight or curving slightly away from one another, gradually and sharply pointed, measuring about 0·25 by 0·012 mm.; basal ray short, straight, conical, about 0·05 by 0·0082 mm, but of course variable.

(3) The "tuning-fork" spicules; with all three rays long, straight, and slender, gradually and sharply pointed; the basal ray longest and stoutest, and the two oral rays running straight forwards, parallel to and almost touching one another, so that the entire spicule is much elongated in the oro-basal direction (fig. 2, *d*). The two oral rays are commonly slightly unequal in length. Total length of an average example, 0·74 mm.; basal ray, 0·42 by 0·01 mm.; longest oral, 0·32 by 0·007 mm.

Quadriradiate Spicules.—These are exactly like the laterally extended sagittal triradiates, with the addition of a very short, straight, sharply pointed apical ray (fig. 2, *g*).

In addition to the principal forms of spicules thus described, various intermediate as well as more or less abnormal forms occur, but these are neither numerous nor important.

2. The Arrangement of the Skeleton (figs. 3—5).

As in all the more highly organised Calcarea Heterocœla, we can divide the entire skeleton into three principal parts,

viz. that of the dermal cortex, that of the gastral cortex, and that of the chamber-containing layer of the sponge-wall between the two. To these may be added the skeleton of the peristome, but this is hardly of sufficient importance to deserve special consideration. The principal part of the skeleton is, of course, that of the chamber layer, which occupies nearly the entire thickness of the sponge-wall, and it is here that we meet with the most surprising peculiarities in structure.

Skeleton of the Dermal Cortex.—The dermal cortex is very thin, and its proper skeleton consists of a thin, confused layer of rather small, slender-rayed, normal sagittal triradiates, lying parallel with the dermal surface, together with an immense number of the minute oxeote "mortar-spicules." Mr. Carter notes the occurrence of small quadriradiates on the dermal surface, but these I have not detected in the small piece which I have examined. They certainly do not play any important part in the formation of the skeleton, and, unlike the large subdermal quadriradiates of the Amphoriscidæ, cannot be regarded as of any systematic importance. The huge oxeote spicules take no part in the formation of the dermal cortex proper, although many of them lie just beneath it. Here and there the dermal cortex is pierced by very stout and densely packed bundles of the long slender oxeotes (intermingled with "tuning-fork" spicules. These bundles (fig. 3, *d. t.*) constitute the expanded (but densely packed) ends of some of the spicular fibres of the chamber layer, which just pierce the dermal cortex and give rise to the characteristic ridges on the outer surface of the sponge. The outermost ends of the spicules are commonly broken off short.

Skeleton of the Gastral Cortex.—The gastral cortex is very much more strongly developed than the dermal, having a thickness of about 0·2 mm. It is composed almost entirely of very densely packed, laterally extended sagittal triradiates, with very long oral rays and very short basals. These spicules are arranged with their longest axes parallel to the gastral surface, but otherwise in the greatest confusion, with the short basal rays pointing in all directions instead of constantly

towards the base of the sponge. This is the only situation in which I have detected quadriradiate spicules, and even here they are few in number, and the apical rays, which project towards the gastral cavity, are very feebly developed. The widely extended oral rays of the subgastral sagittal triradiates may also be regarded as taking part in the formation of the gastral cortex, but these spicules are best considered in connection with the next portion of the skeleton.

Skeleton of the Chamber-bearing Layer.—The part of the sponge lying between the gastral and dermal cortex and containing the flagellated chambers is, in the piece examined by me, a little over 4 mm. in thickness, the total thickness of the sponge-wall being about one sixth of an inch. Its skeleton is very strongly developed, and (excluding the triradiates which line the large exhalant canals, and which resemble more or less those of the gastral cortex) it consists of the following parts:

(a) The subgastral sagittal triradiates. Very well developed and abundant; occupying the normal position, with widely extended oral rays lying beneath the gastral cortex, and long straight basal rays penetrating the chamber layer more or less vertically or obliquely (fig. 4).

(b) The spicular fibres (figs. 3—5, *fi.*). These consist of long bundles of the characteristic slender, elongated, "tuning-fork" spicules. The component spicules are closely packed together side by side, parallel with one another (fig. 4). So closely are they packed together that in a stout fibre it is very difficult to make out the outlines of the individual spicules. There does not seem to be any special connecting substance analogous to the spongin of siliceous sponges, but the spicules appear to be held together simply by the gelatinous ground-substance of the mesoderm. The arrangement of the fibres is very similar to that of the spicular fibres in many siliceous sponges. They do not simply run through the wall of the sponge from gastral to dermal surface, but they run in every direction, and, by frequently coming in contact and crossing one another at all sorts of angles, give rise to a loose, irregular network (fig. 3). The thickness of the fibres

is very variable, according to the number of spicules entering into their composition at any given point. They are seldom more than about 0·07 mm. in diameter, except towards the dermal surface, where their thickness may be greatly augmented by the addition of numerous slender oxeote spicules as already mentioned. Towards the gastral surface the fibres often appear, as it were, to spring from the long basal rays of the subgastral sagittal triradiates (figs. 4, 5), a relation which is of considerable importance in considering the derivation of this peculiar type of skeleton from the primitive articulate type. Except just close to the two surfaces of the sponge-wall the fibres appear to consist solely of the remarkable tuning-fork-shaped triradiates. All the spicules of any one fibre, so far as I have been able to make out, have their basal rays pointing in the same direction. Usually the fibres have a distinct, though more or less oblique trend from gastral to dermal surface, and it is extremely interesting to note that the basal rays of the component spicules in such cases almost always point towards the outside of the sponge, a fact which has already been noted by Mr. Carter.

(c) The huge Oxeote Spicules. These occur in immense numbers, disposed in the utmost confusion between the spicular fibres (fig. 3). The thickness of each one is greater than that of an average fibre, and, indeed, the fibrous portion of the skeleton can only play a part of secondary importance in strengthening the sponge-wall as compared with these giant spicules.

Skeleton of the Peristome.—This appears, from Mr. Carter's description, to present no very characteristic or important features. It consists of long, straight, slender oxeote spicules arranged perpendicularly (parallel to the long axis of the sponge). The lower ends of these spicules are crossed at right angles and supported by the outspread lateral rays of the gastral triradiates.

c. The Canal System.

The canal system of Lelapia australis conforms in all respects to the typical Leuconoid arrangement, the entire sponge being, as already pointed out, a single Leuconoid individual. The flagellated chambers are spherical or ovoid, only about 0·06 mm. in diameter and frequently less. They are thickly scattered in the transparent, gelatinous, mesodermal ground-substance which separates the branches of the inhalant and exhalant canals. Their exhalant openings are, as usual, circular and well-defined, each with a delicate chamber-diaphragm. The prosopyles, which are not very easy to make out in small Leuconoid chambers, I have not succeeded in detecting.

The inhalant canal system is irregular and more or less lacunar. Owing to the feeble development of the dermal cortex, there is no separately recognisable cortical canal system. The inhalant pores are small and scattered over the dermal surface. They open into short canals which unite to form larger trunks before penetrating the deeper parts of the sponge-wall, but there appears to be nothing definite about the arrangement. The smaller exhalant canals collect into large trunks, which run to open on the gastral surface, piercing the gastral cortex more or less at right angles. The wider parts of these trunks are lined by a layer of laterally extended sagittal triradiates, similar to those of the gastral cortex, and amongst them may be seen sagittal triradiates like the subgastrals, with long basal rays projecting into the surrounding tissue at right angles to the course of the canal. These facts argue in favour of the supposition that the larger exhalant canals in Lelapia may be formed by pitting in or folding of the gastral surface. The openings of the exhalant canals (fig. 6, *ex. ap.*) into the wide gastral cavity are abundantly scattered over the inner surface of the gastral cortex, and are provided with membranous diaphragms, as Mr. Carter has already pointed out. From the gastral cavity, of course, the water

finds its way out of the sponge through the wide, terminal osculum (fig. 1, *osc.*).

The histology of the sponge, so far as the condition of the specimen will permit of investigation, offers no features of special interest, and appears to agree with that of other Heterocœla. Beyond the transparent gelatinous ground-substance of the mesoderm, the contracted collared cells, and the nuclei of the pavement epithelium lining the canals, I have not been able to make out any details.

III. Relationships of Lelapia.

A. Relationships to other recent Heterocœla.

The canal system of Lelapia australis, as already pointed out, offers no features of peculiar interest and, as regards its probable derivation from the more primitive Syconoid type, stands on exactly the same footing as the canal system of any other Leuconoid Heterocœle. As the probable mode of derivation of the Leuconoid from the Syconoid type has already been discussed in my memoir on the structure and classification of the Heterocœla (1), it is unnecessary to enter further into the question in this place.

The skeleton, however, is very peculiar, and, at first sight, may seem to place great difficulties in the way of believing in the Syconoid ancestry of Lelapia. These difficulties, however, disappear upon closer examination.

The peculiar form of the "tuning-fork" spicule is not, in itself, of much significance, and, as already pointed out by other writers, it is paralleled more or less closely in Haeckel's Leucandra (Leucortis) pulvinar and L. (Leucetta) pandora (4), both of which are recent species; while it is also met with in the fossil Sestrostomella rugosa and S. clavata described by Dr. Hinde (5). In none of these, however, does it appear to attain to anything like the degree of development met with in Lelapia australis. The tendency of the triradiate to vary is well known, and we meet with a

modification perhaps even more remarkable in my Grantiopsis cylindrica (1).

As I have previously pointed out, the arrangement of the skeleton in the Calcarea Heterocœla is of more importance for purposes of classification than the mere form of the component spicules, and the difficulty lies in explaining how the very peculiarly arranged skeleton of Lelapia can have been derived from a Syconoid ancestor with its characteristic articulate tubar skeleton.

We may, however, at once confine our attention to the skeleton of the chamber-bearing layer, for that of the dermal and gastral cortex differs in no essential points from the corresponding parts in other corticate Heterocœla. Taking first the subgastral sagittal triradiates, we find in these a strong argument in favour of our view, for they exactly correspond to the similar spicules of the typical articulate skeleton. These spicules, indeed, seem to be wonderfully persistent, being also met with, as I have already pointed out, in the genus Leucandra, after all other traces of the articulate tubar skeleton have disappeared.

The huge oxeote spicules are probably, like the very similar spicules of some species of Leucandra (e. g. L. cataphracta, Haeckel), to be regarded as incursions from the dermal cortex, the dermal surface being the characteristic position for oxeote spicules.

We have left the spicular fibres, whose presence distinguishes Lelapia australis from all other known recent sponges. These I believe to be derived from the articulate tubar skeleton of a Syconoid ancestor. The arguments in favour of this view are as follows:—(1) The position of these spicules with regard to one another is the same as in the typical articulate tubar skeleton, i. e. with their basal rays parallel, overlapping, and all pointing in the same direction. (2) The position of the spicules with regard to the gastral and dermal surfaces is, when the position of the fibre as a whole allows of it, almost invariably the same as in the articulate tubar skeleton, i. e. with the basal rays pointing to the dermal surface. (3) The

relations of the subgastral sagittal triradiates to the fibres is, in many cases at any rate, identical with that of the corresponding spicules to the articulate tubar skeleton of a Syconoid.

Thus, while in Leucandra the spicules of the primitive articulate skeleton become scattered and disjointed, in Lelapia they retain their mutual relationships, and indeed become much more intimately associated with one another to form spicular fibres,—this formation of fibres being greatly facilitated by their very peculiar shape. The fibres as a whole, however, become irregularly arranged, as do the individual spicules of Leucandra.

Thus, then, I see no reason for altering the systematic position of the genus Lelapia as given in the genealogical tree at the end of my previous memoir (1). In other words, I regard Lelapia as an offshoot from the great family Grantidæ, coming off from the same branch which gave rise to the genus Leucandra. At the same time this way of thinking would not prevent us, if necessary, from accepting the Pharetrones as a distinct family and including Lelapia therein.

B. Relationships to the Fossil Pharetrones.

Professor Zittel, in his classical "Studies on Fossil Sponges" (3), accepted Haeckel's division of the Calcarea into Ascones, Leucones, and Sycones, but added thereto a new family, Pharetrones, which he regarded as of co-ordinate systematic value with Haeckel's three groups. The following diagnosis was given of the new family:—"Wand dick, mit ungeraden Astcanälen oder ohne alle Canäle. Skeletelemente zu anastomosirenden Fasern angeordnet. Dermalschicht häufig vorhanden."

In this family Zittel placed, with one exception (Protosycon), all the then known fossil Calcarea, amounting to no less than fifty genera, and ranging from the Devonian to the Upper Chalk.

These numerous fossil genera are naturally very imper-

fectly known, and even their calcareous nature has been disputed. This was largely owing to the fibrous character of the skeleton, which was not then known to occur in any living calcisponge, and certainly appeared to indicate a siliceous nature for the Pharetrones.

In 1882, however, Dr. Hinde published a valuable paper (5) in which this question was fully discussed, and described more or less in detail the spiculation of five species of so-called Pharetrones from the Cretaceous and Upper Greensand formations. These observations sufficiently proved the calcareous nature of at any rate these five species, for characteristic triradiate and quadriradiate spicules were detected.

The first species described by Dr. Hinde is Verticillites d'Orbignyi. The description and figures clearly prove this to be a calcareous sponge, but I do not think that there is the slightest evidence in favour of regarding it as a Pharetronid. It is a very thin-walled sponge, and the portions of the skeleton described are evidently simply the dermal and gastral cortex respectively. The latter is very strongly developed and differs in no essential respect from that of many living Heterocœla, being composed of a dense feltwork of triradiate spicules with aborted basal rays. This layer is pierced by the circular exhalant apertures leading into the gastral cavity, which, being placed near together, give the gastral cortex a reticulate character. To apply the term fibrous to this skeleton appears to me to be a mistake; it is no more fibrous than that of many living Heterocœla, and the so-called fibres are certainly not homologous with the spicular fibres of Lelapia. Verticillites d'Orbignyi ought, then, to be removed from the Pharetrones altogether. The thinness of the sponge-wall and the regular disposition of the exhalant openings on the gastral surface suggest that it may have possessed a Syconoid canal system, while the presence of quadriradiates in the dermal cortex, with inwardly projecting apical rays, suggests a position amongst the Amphoriscidæ of my classification.

In the next two species, again, Corynella rugosa and C.

socialis, the evidence placed before us does not seem to be conclusive as to the truly fibrous character of the skeleton, apart from the so-called fibres of the cortical one.

In the two species of Sestrostomella, viz. S. rugosa and S. clavata, described by the same author, there appears, on the other hand, to be little doubt as to the existence of a truly fibrous skeleton distinct from the cortical one. The fibre itself, to quote the words of Dr. Hinde, "exhibits an altogether different character in the form and arrangement of the component spicules from that which prevails in the examples of Verticillites and Corynella, already described." The ensuing description, however, also shows that the fibre is very different from that of Lelapia. "The central portion of the fibre generally appears to be occupied by a large tri- or quadriradiate spicule, one ray of which extends along the central axis of the fibre. . . . Beyond this centrally-placed large spicule the remaining portion of the fibre appears to be composed of several different forms of triradiate spicules, whose rays are so compactly and intricately interlaced together that it is extremely difficult to ascertain their complete forms with any degree of precision." Amongst these smaller spicules occur fork-shaped triradiates somewhat similar to those of Lelapia, but they appear to be irregularly arranged. In view of the occurrence of these spicules in other recent Heterocœla, as already mentioned, their systematic value must be considered as very questionable.

Lelapia, then, does not appear to be very closely related to any of the fossil Pharetrones described by Dr. Hinde. Whether it is more closely related to any of the other numerous fossil sponges which have been included in that group, it is impossible, in the absence of detailed information as to the form and arrangement of the spicules in the latter, to decide. It has, however, a truly fibrous skelelon; and in this respect it agrees with the main character of the family Pharetrones as laid down by Zittel. We may therefore regard it as a living representative of the group, but whether the group itself, as it stands, is a natural one is another question altogether, and one

which, owing to the state of preservation of the fossils, will perhaps never be decided.

Zittel (3) regarded his Pharetrones as the ancestral forms from which the living calcareous sponges (Ascones, Leucones, and Sycones of Haeckel) originated. I need hardly say that I do not agree with this view, and I have endeavoured to show in this paper how a "spiculo-fibrous" skeleton may have been derived from the more primitive Syconoid type. My arguments, however, obviously apply only to the case of Lelapia, for the minute structure of other calcareous sponges with a fibrous skeleton is not sufficiently well known to justify speculation as to their origin. Thus it is possible that the fibres of those Pharetrones which are described by Zittel as consisting of bundles of parallel oxeote spicules are really composed of elongated, fork-shaped triradiates. Even in Lelapia it is hard to distinguish these, in situ, from oxeote spicules, owing to the closeness with which they are packed together; and in a section of a fossil sponge it would be impossible to do so unless one happened to get a section passing just through the fork of the spicule and in the plane of all three rays.

All things considered, then, it seems unadvisable, in the present state of our knowledge, to introduce the family Pharetrones into our system of recent Calcarea, and Lelapia may be regarded simply as a very specialised type of the Grantidæ.

Melbourne, November, 1893.

Reference List of Literature.

1. Dendy.—"Studies on the Comparative Anatomy of Sponges: V. Observations on the Structure and Classification of the Calcarea Heterocœla," 'Quart. Journ. Micr. Sci.,' vol. xxxv, N. S., p. 159.

2. Carter.—"Descriptions of Sponges from the Neighbourhood of Port Phillip Heads," 'Annals and Magazine of Natural History,' vol. xviii, ser. 5, p. 126.

3. Zittel.—"Studien über fossile Spongien, Dritte Abtheilung," 'Abhandlungen der k. bayer. Akademie der W.,' II Cl., Bd. xiii, Abth. ii, 1878.

4. Haeckel.—'Die Kalkschwämme.'

5. Hinde.—"Notes on Fossil Calcispongiæ, with Description of New Species," 'Annals and Magazine of Natural History,' vol. x, ser. 5, p. 185.

DESCRIPTION OF PLATE 13,

Illustrating Dr. Dendy's paper "On the Anatomy of Lelapia australis."

Reference Letters.

a. Large oxeote spicules. *b.* Long slender oxeote spicule. *c.* Small oxeote spicules ("Mortar-spicules"). *d.* Tuning-fork-shaped triradiates. *e.* Normal sagittal triradiates. *f.* Laterally extended sagittal triradiates. *g.* Quadriradiate. *d. c.* Dermal cortex. *d. t.* Dermal tuft of triradiates and slender oxea. *ex. ap.* Openings of exhalant canals into central gastral cavity. *ex. c.* Exhalant canal. *fi.* Spicular fibres formed of tuning-fork-shaped triradiates. *g. c.* Gastral cortex. *osc.* Osculum. *s. g. s.* Subgastral sagittal triradiates.

(The spicules are delineated in blue throughout.)

Fig. 1.—Lelapia australis. (From a sketch by Mr. H. J. Carter, F.R.S.)

Fig. 2.—Isolated spicules, from a preparation boiled out with caustic potash. Only the two ends of the large oxeote (*a*) are drawn. All are drawn to the same scale, under Zeiss C, ocular 2, camera.

Fig. 3.—Skeleton arrangement, as seen in a thick, unstained, longitudinal section. × 25.

Fig. 4.—Portion of the gastral cortex and adjacent skeleton of the chamber-bearing layer, as seen in a thick, unstained, longitudinal section. Drawn under Zeiss C, ocular 2.

Fig. 5.—Portion of a subgastral sagittal triradiate, showing its relation to a very slender fibre formed of tuning-fork-shaped triradiates. Drawn under Zeiss C, ocular 2.

Fig. 6.—Portion of a transverse section, stained with borax carmine and cut by the paraffin method. × 25. Each flagellated chamber is represented by a red spot.

Appendix.

I take the present opportunity of correcting a few slight misprints which occur in the last paper of this series, "On the Structure and Classification of the Calcarea Heterocœla."

Page 163, line 2, *for* "caused" *read* "lined."
" 166, " 16, *erase* the comma after the word "to."
" 166, " 34, *for* "strobulus" *read* "strobilus."
" 167, " 17, *for* "Bauerbank" *read* "Bowerbank."
" 168, " 15, *for* "tuber" *read* "tubar."
" 168, " 24, *for* "fig. 8" *read* "fig. 5."
" 169, " 34, *for* "cram" *read* "crown."
" 171, " 11, *for* "non-" *read* "inter-."
" 176, " 2, *for* "situated" *read* "inflated."
" 179, " 3, *for* "Syllectoid" *read* "Sylleibid."
" 195, " 11, *for* "strangely" *read* "strongly."
" 206, " 28, *for* "Lycetta" *read* "Sycetta."
" 208, " 4, 5, 6, *for* "Heterocœla Calcarea" *read* "Calcarea Heterocœla."
" 216, " 3, *for* "into" *read* "on to."
" 217, " 12, *for* "permanent" *read* "pavement."
" 229, " 9, *for* "van" *read* "von."
" 232, " 16, *for* "Thabden" *read* "Rhabden."

The Structure of the Bill and Hairs of Ornithorhynchus paradoxus; with a Discussion of the Homologies and Origin of Mammalian Hair.

By

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(With Plates 14, 15, and 15A.)

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I. Introduction.

In the summer of 1884 I made a communication "On the Tactile Terminal Organs and other Structures in the Bill of Ornithorhynchus" to the meeting of the Physiological Society at Oxford. A short account, containing however the chief results, was published in the Proceedings of the Society ('The Journal of Physiology,' 1884, pp. 15, 16). In searching for the terminations of the abundant medullated nerves I found two remarkable structures in the epidermis of the bill:—(1) Epithelial rods which appear to convey the effect of surface pressure to a group of nerve end organs resembling Pacinian bodies. These rods, from their obvious analogy to the push of an electric or, better still, pneumatic bell, may be conveniently called "push-rods." (2) Other epithelial rods along the axis of which passes the duct of a gland. These rods resemble in certain respects a shortened and truncated hair.

The interpretation of these latter rods as modified hairs was disputed at the meeting by Dr. Klein, but supported by Professor Schäfer. This controversy and the obvious interest of the inquiry led me to undertake further work, which included an investigation of the hairs covering the body of this animal. From time to time this work has been continued from 1884 up to the present date (December, 1893), and many drawings have been made and discussed with friends, although until now I have published nothing more upon the subject. During the summer of last year (1892) I worked for some weeks in the laboratory of my friend Professor Lankester, at which time the drawings were arranged and the description of Pl. 14 written.

Within the last few days the recent description of the push-rods by Professor J. T. Wilson and Mr. C. J. Martin ('Macleay Memorial Volume,' pp. 190—200) has reached me. I was prepared to find that their investigation would have rendered any further publication on this point unnecessary, inasmuch as fresh material had been available, the want of which had confronted me throughout, and especially in the attempt to

trace the endings of the nerves. The authors have, however, relied almost entirely upon photomicrography for their illustrations, with the result that the figures upon two (xxiv and xxv) out of the three plates are utterly worthless, and convey a most inadequate conception of the appearances presented by the sections. It is evident from the descriptions that the sections relied upon were adequate, and perhaps the negatives and the first impressions were also satisfactory: but in the form in which the paper reaches the public there is something inconsistent in the confident references made in the text to the representation of detail in a figure which turns out on inspection to be the merest smudge (see especially fig. 5, pl. xxiv, which, among all figures ever published in scientific papers, must surely take the palm for obscurity). My sympathies are entirely with those who have been misled into trusting a process which for this purpose appears to be entirely useless. The authors have, however, made some drawings, the photographic representations of which are infinitely better than those of the sections. Fortunately, too, these figures, which are all to be found on the last plate (xxvi), deal with points of structure which needed the fresh tissues for their adequate treatment, and are therefore unrepresented among my illustrations.

I therefore propose to publish my figures together with their explanation (in the "Description of Plates") exactly as I wrote them in 1892, except for mere verbal corrections, &c. Thus my description of the push-rods is entirely independent of that recently published in Australia, although it will be found that the two accounts are in substantial agreement.

The gland-ducts and their associated hair-like and nervous structures are not alluded to by the above-mentioned authors. This is to be regretted, inasmuch as many of the most important points can only be decided by the use of the fresh tissues. A detailed description of these, so far as it is possible with the material at my disposal, is also given below, and the same is true of the hairs covering the body of the young and mature animal.

The material upon which all the work described below has

been done consisted of (1) parts of the bill hardened in chromic acid by the late Professor Moseley in 1874, at the same time that he prepared the tongue which I have described in this journal (see 'Quart. Journ. Micr. Sci.,' July, 1883, p. 453, for further details concerning this material), and the horny teeth (see 'Quart. Journ. Micr. Sci.,' July, 1888, pp. 31, 32); (2) a specimen kept many years in spirit in the Oxford University Museum, the ovary of which was described in this journal (January, 1884, p. 118); other similarly preserved specimens in the Museum were also employed; (3) the young Ornithorhynchus of which I was enabled to describe the true teeth through the kindness of the late Professor W. K. Parker ('Quart. Journ. Micr. Sci.,' July, 1888, pp. 10, 11). This latter specimen was 8·3 cm. long in the curled-up attitude in which I received it, and the larger hairs had alone appeared above the skin.

Since the above was written I am enabled, through the kindness of Professor W. N. Parker, to supply figures of the natural size of the young specimen of Ornithorhynchus referred to above. The appearance from the left side is seen in Plate 15A, fig. 1, from the ventral aspect in fig. 2. The latter has been already published, reduced one half, by the late Professor W. K. Parker. The drawings from which Pl. 15A was prepared were made by Mr. M. P. Parker. The considerable amount of work which has been already published upon material from the single specimen here figured is indicated in the following list of memoirs:

G. B. Howes.—'Journ. Anat. and Physiol.,' 1886, xxi, p. 190. Describes and figures the shoulder girdle.

G. B. Howes.—'Journ. Anat. and Physiol.,' 1892, xxvii, p. 543. Describes the pelvis, and figures a section of it.

The late W. K. Parker.—"Mammalian Descent," London, 1885. Describes some of the external characters (p. 48, et seq.), and figures the ventral view of the specimen one half the natural size (p. 25). This same view is represented the full size in Pl. 15A, fig. 2, accompanying this paper.

W. N. Parker.—'Brit. Association Reports,' 1891, p. 693. Compares the snout with that of the young Echidna.

W. N. Parker.—"On some Points in the Structure of the Young of Echidna aculeata," 'Proc. Zool. Soc. Lond.,' read January 16th, 1894, and to be published shortly. Compares with young Echidna, especially as regards "Jacobson's organ," a section of which is figured.

E. B. Poulton.—'Proc. Roy. Soc.,' 1888, xliii, p. 353. Describes the true teeth, and figures a section of one.

E. B. Poulton.—'Quart. Journ. Micr. Sci.,' 1888, vol. xxix, p. 9. Describes the true teeth, and figures their appearance, in sections, and in minute structure.

R. Wiedersheim.—'Zeit. f. wiss. Zool.,' liii, 1892, suppl., p. 43. Describes and figures the pelvis.

This paper having been prepared for the press at a time of great pressure, my friend Dr. Benham has very kindly relieved me of the labour of writing the historical part of the two latter sections. I also wish to thank my friend Professor Howes for kindly suggesting certain lines of recent research which bore upon the subject. So far as the earlier sections are concerned, with the exception of Wilson's and Martin's recent paper there is no other record worthy of mention.

II. The Push-rods.

It will not be necessary to describe the histological details of these structures at any great length. Reference to Pl. 14 and to the full descriptions will be sufficient. I shall therefore chiefly dwell upon the points which are not touched by Wilson and Martin, or in which my interpretation differs from theirs.

The proportion of these structures to the gland-ducts varies in different parts. Thus on the presumably highly sensitive ridges within the lower jaw the former are the more numerous, as may be seen by glancing at fig. 5, where the push-rods are seen in section as circles. On the external surface of the bill, however, these proportions are usually reversed. In relation to the sensitive condition of the bill we learn with great interest that it is, in the living state, covered with "smooth, soft, and humid skin" ("Anatomy of the

Muzzle of the Ornithorhynchus," by Professors J. T. Wilson and C. J. Martin; 'Macleay Memorial Volume,' p. 180). In this country, where we see only dry or spirit-preserved specimens, it has generally been looked upon as a tough, horny structure. The glands to be described below are doubless responsible for the humidity, although they may also, as I have suggested ('The Journal of Physiology,' 1884, p. 16), secrete a substance which protects the skin from the prolonged action of water.

Wilson and Martin describe structures in the horny teeth which they believe to represent push-rods which have undergone cornification (l. c., p. 192).

In offering this interpretation I believe that they have mistaken for push-rods the columns of cells which extend from the summits of the numerous papillæ towards, and often as far as, the surface. These cells are much less cornified than those around, and stain readily; furthermore it may be said that the columns "show a series of imbricated superposed cells," although the arrangement differs in various details from that of the push-rods. The fact that a column invariably extends from the summit of a papilla, while a push-rod is invariably surrounded by two or more papillæ, is sufficient proof that the two structures are not homologous. The structure of the cell-columns and their relation to the papillæ are clearly shown in my paper already quoted ('Quart. Journ. Mic. Sci.,' July, 1888, Pl. IV, figs. 4, 5, 8, 10, 11).

Speaking of the dermal sheath which surrounds the lower part of each push-rod, the above-quoted authors regard the rod as an epithelial downgrowth which causes "a depression in the summit of a dermal papilla" (l. c., p. 193). Inasmuch as two or more distinct papillæ arise from the upper edge of the dermal sheath (to be seen in section in Pl. 14, fig. 3, accompanying this paper; and, by the eye of faith, in pl. xxiv, fig. 6, of the 'Macleay Memorial Volume'), I should prefer to regard the rod as a modified interpapillary process, with the surrounding papillæ united into a continuous sheath below, while they remain free above.

The shaft of a push-rod consists of four concentric layers of cells, which are rendered quite distinct by their unequal staining (figs. 3 and 4). Wilson and Martin regard the outermost of these layers as belonging to the general epidermis, and forming "a kind of follicle" round the rod proper. I took the same view in 1884, speaking of the third layer as "followed by concentrically arranged fusiform cells belonging to the general epidermis" (l. c., p. 16). The innermost imbricated cells, constituting the first layer, are looked upon by Wilson and Martin as hollow truncated cones made up of three or more cells. This interpretation is certainly supported by the teased preparation represented in their pl. xxvi, fig. 17. I could never make out any cell outlines in this layer when studied in transverse sections of the rods, although three or more nuclei were often seen (fig. 3). Longitudinal sections, on the other hand, show the outlines of successive cells very distinctly (fig. 4). My observations to this extent support Wilson's and Martin's conclusions as to the nature of the innermost cell-structures. As to the second layer of imbricated cells, and the larger far less sloping cells constituting the third layer, we are in entire agreement, and my fig. 4 would, in this respect, serve for the illustration of Wilson's and Martin's description. It should be noted, however, that the nuclei of the cells of all the layers are surrounded by pigment masses and granules.

The central group of fine filaments occupying the axis of the rod, together with the ring of similar structures placed between the first and second layers of imbricated cells, are very conspicuous, and early attracted my attention (1884, l. c., p. 16). They are clearly seen in figs. 3 and 4. Longitudinal sections show that they pursue a parallel course along the rod except at the convex lower extremity, where I could just make out, in the most favorable preparations, that the filaments of the central group diverge in a brush-like manner (fig. 1). The most careful examination, under very high powers, of the best material I could command, displayed a structure which is represented in fig. 4. Each filament appeared to be

made up of short sections corresponding in length to the thickness of the adjacent imbricated cells. From this structure I formed the conclusion that the filaments are probably built up of units contributed by the cells which lie outside them. Wilson and Martin describe them as made up of bead-like varicosities, each of which is placed between a pair of cells (simple or compound) in vertical succession (l. c., pl. xxvi, fig. 15, for a diagrammatic representation). At the meeting of the Physiological Society (1884) I suggested that the filaments might be nerve terminal organs, and that the imbricated arrangement of cells around them might result in pressure whenever the free surface of the rod was in contact with external objects, thus effecting the stimulation of the nerve. Professor Schäfer pointed out, in the discussion, that the highly refringent character of the filaments is opposed to the view that they are terminal nerve-fibrils. I have often tried to find a connection with the abundant nerves below the base of the push-rod, but such an investigation needs the fresh tissues. Wilson and Martin now describe the filaments as naked axis-cylinders prolonged from the nerve-fibres below the rod, which suddenly lose their medullary sheaths soon after entering the epithelium. Although their drawings from gold-stained preparations (pl. xxvi, fig. 21) appear to leave no doubt that the filaments are connected with nerves and form some kind of terminal organ, it is obviously erroneous to speak of them as "naked axis-cylinders" (p. 196) or "nerve-fibrils" (p. 197). They are highly refringent and have none of the characters of these nerve structures. It is noteworthy, too, that although the filaments are represented in pl. xxvi, fig. 22, as black varicose threads, the authors accurately state in the description (p. 200) that the fibrils "are not black, but only highly refracting." Furthermore, if the photomicrographs establish nothing else, they certainly prove that this conclusion as to the nature of the filaments is erroneous; neither naked axis-cylinders nor nerve-fibrils could have caused the appearances seen in transverse section in pl. xxv, fig. 13, and in longitudinal section in fig. 8.

These authors state (p. 196) that I failed to recognise the

nervous character and connections of the filaments. I am in entire agreement with this statement: "the nervous character" does not exist, and the nervous connections could not by any possibility have been seen in the tissues with which I was supplied. Although I did not recognise connections which could not have been seen, I certainly inferred them, as the title of my communication indicates ("On the Tactile Terminal Organs," &c., 'Journ. of Physiology,' 1884).

The filaments must be regarded as remarkable terminal organs, entirely distinct in histological nature from the axis-cylinders which terminate in them; and Wilson and Martin's fig. 25 seems to suggest that the change in nature takes place at or close to the point at which the medullary sheath disappears. The appearance presented by the filaments is very clearly shown in figs. 3 and 4 accompanying this paper. They must be looked upon as a new and interesting form of nerve terminal organ, probably epithelial in origin.

As regards the Pacinian-like bodies, Wilson and Martin support my previous account, but they also describe certain larger forms of these structures, rather more deeply placed than those immediately below the push-rods. Bodies similar to those beneath the rods occur in the mouth, and were described and figured in some detail in my paper on "The Tongue of Ornithorhynchus" in this Journal ('Quart. Journ. Micr. Sci.,' July, 1883, Pl. XXXII, fig. 5).

The constant occurrence of a group of Pacinian-like bodies at the base of each push-rod (figs. 5 and 6) is of great physiological interest, as it strongly supports the view—widely held but as yet unproved—that the function of this form of nerve end-organ is to aid the nervous system in the appreciation of pressure. The obvious use of the push-rods is, as I stated in 1884, "to supply specially moveable areas yielding to surface pressure, which is thus communicated to the terminal organs below."

Another interesting end-organ described by these authors is placed among the epidermic cells of the base of the rods. In these "lenticular bodies" the axis-cylinder is described as

ending in a disc which separates "two clear vesicular cell-like structures." This form of ending evidently needs the fresh tissues for its demonstration.

At first sight the push-rods appear to be modified hairs, but the examination of their minute histological details does not support this comparison. It is possible, however, that they may be found to have some bearing upon the recent suggestion that the Mammalian hair corresponds to an epidermic tactile organ of the lower Vertebrata. However this may be, the resemblance to the Mammalian hair as it now is, in my opinion, is far less close than that of the epidermic structures associated with the ducts of glands which open on the surface of the bill.

Souza Fontes, in 1879 ('Beit. z. Anat. Kenntniss der Hautdecke des Ornithorhynchus,' Inaug. Dissert., Bonn), mentioned and figured these structures and the gland-ducts described below, but the paper is quite unworthy of mention. Indeed, the principal feeling evoked by a glance at the Plate is one of surprise at the system which can confer a University Degree for such a production.

III. The Gland-ducts of the Bill and Structures associated with them.

The gland-tubes of the bill, and, indeed, of the general body surface, closely resemble the Mammalian sweat-glands, the secretory part of the tubule being wider than the duct, and lined with short columnar cells surrounded by a longitudinal layer of smooth muscle-cells (fig. 8, *gld.*). The wall of the duct is composed of nucleated, probably polyhedral, cells, indistinctly marked off from one another in my sections. These cells are separated from the lumen by a cuticle, represented as a row of thin, deeply staining, plate-like structures resembling nuclei (fig. 8, *d'*, transverse section; below *d* longitudinal section). Externally the tubes are surrounded by a membrana propria, in which nuclei are especially distinct in the transverse section of the duct (*d'*).

The existence of such typical structures in the most primitive mammal indicates that sweat-glands are among the most

ancestral features of the Class. Although the hairs of Ornithorhynchus will be shown below to present many peculiarities which are, as I believe, ancestral, the sweat-glands are essentially similar to those of Mammalia generally.

In the bill, the deeply placed coiled gland-tube is succeeded by a coiled duct which, as in many other mammals, enters the base of an epidermic downgrowth—the interpapillary process (fig. 8). The epidermic process itself, however, is by no means typical, but presents many special peculiarities, some of which support the conclusion that it is a modified hair,—sharply cut off above at the level of the uppermost epidermic layer, shortened below by retraction of the hair-bulb, so that the latter descends but a short distance beneath the lowest layer of the epidermis (figs. 8, 13—16). Nevertheless, in the young Ornithorhynchus the bulb-like part of the structure extends to a somewhat deeper level (compare fig. 16). These hair-like structures were briefly described in 1884 (l. c., p. 16, where, however, in line 11 from bottom, the words "hair papilla" are obviously intended for "hair-bulb").

The epidermic processes are, like the push-rods, surrounded below by a continuous dermal sheath, the upper edge of which gives rise to several papillary upgrowths (figs. 8, 13—15 for longitudinal, figs. 9—12 for transverse, section). The process is continued upwards through the stratum corneum as a cylinder—either straight or with S-like curves,—which remains perfectly distinct from the epidermis around, being separated by a downgrowth of cells so marked that their direction becomes vertical. In this respect the structures in question resemble the push-rods (compare fig. 1 with fig. 8). At its upper free end this cylinder is sharply truncated so as to be flush with the surface of the bill. But in favorable examples it is surrounded by a distinct circular depression, and it may even project a little above the general surface (figs. 8, 13, and 15). At the posterior part of the upper bill the upper ends of the cylinders are remarkably expanded, so that their outline becomes funnel-shaped (fig. 14). The S-like curves into which many of the cylinders are thrown

in their passage to the surface are exceedingly characteristic in appearance (figs. 13 and 15).

The cylinder itself is hair-like in structure, being composed of elongated fusiform cornified cells in which traces of a nucleus, surrounded by pigment, can be detected (fig. 8). The lumen of the duct traverses the axis of the corneous cylinder, and is star-like in transverse section (figs. 9 and 10). The cells near the cylinder are disposed in concentric circles round it (fig. 9). Tracing the cylinder downwards into the inter-papillary process, we find many points of resemblance to a hair. The general epidermis is continued over it as a sheath, which strongly suggests the outer root-sheath of a hair, and between it and the cylinder itself a line of separation tends to appear (fig. 8, *o. r. s.*, and also at level c; see also fig. 10). Below, this sheath forms the outer part of the bulb, and is separated from the inner part by a space containing small branched cells, the nature of which could not be determined in my material (fig. 8, *sp.*, and fig. 13). The cells of this outer sheath are richly pigmented, like, or even more than, those of the lower layer of the general epidermis with which they are continuous (figs. 8 and 10). Within this sheath the cylinder is surrounded by a distinct layer composed of flattened cells, shown by transverse sections to be two or more deep, but varying in thickness in different parts (fig. 10, fig. 11, *c.*; compare also fig. 8, *c.*). This layer may represent the inner root-sheath, or the cuticle of the hair, or both of these together. It is continued over the inner part of the bulb, and separates the latter from the space described above (fig. 8, *sp.*). Within this layer the cylinder consists, as described above, of fusiform corneous cells arranged longitudinally; below, these elements pass into polyhedral cells, staining in carmine, &c. The inner part of the bulb is made up of these latter, and presents the strongest possible resemblance to the bulb of a hair (figs. 8 and 11). In certain slender cylinders which occur intermixed with the others, this part of the bulb appears to be wanting (fig. 15).

In the upper part of the bulb, and for a variable distance above it, the duct is lined by a single layer of distinct cubical

cells (fig. 8), and it coils in a very characteristic manner in the neck and upper part of the bulb (fig. 13; in fig. 8 the coiling is only slightly marked; figs. 14 and 15 represent peculiar forms in which this character is not present). The coiled duct passes downwards into a straight section resembling the gland duct in the dermis with which it is continuous below the bulb (fig. 8). It was, however, impossible to establish the existence of a cuticle to the duct in the bulb, although the inner part of the cells immediately round the lumen stained far more deeply than the outer part (fig. 11, *d'*.).

Immediately below the whole bulb the duct is invariably surrounded by a large ganglion containing abundant medullated nerve-fibres showing Ranvier's nodes, and large ganglion-cells (figs. 8 and 12). This ganglion is surrounded by a fibrous sheath which appears to be prolonged from the dermal sheath (corresponding to the hair-sac) of the hair-like cylinder. Large nerves are seen entering the ganglion, the sheath of which is continuous with their epineurium (fig. 8). The duct which pierces the ganglion is separated from it by a distinct fibrous sheath, clearly shown in transverse section (fig. 12) but very thin in the longitudinal (fig. 8). This sheath appears also to be derived from the layer corresponding to the hair-sac, and to be continuous with its inner part, while the ganglionic sheath is continued from its outer (fig. 8). This, at least, appears to be the probable interpretation of the appearances represented in fig. 8; but the whole structure of these hair-like epidermic cylinders, and the nervous tissues evidently associated with them, is so remarkable and complex that the fresh tissues are required for their satisfactory elucidation and for the discovery of the nerve terminations which we must believe to exist in connection with the apparatus.

I believe that this account represents all that can be ascertained by the careful examination of the available material, and that it supports the conclusion I suggested in 1884—that the gland ducts of the bill reach the surface by entering the bulbs and by advancing along the medulla of shortened and degenerate hairs. Such an opinion is further confirmed by the

fact which will be established below that the corresponding glands of the general body surface of this animal bear a constant relationship to the larger hairs.

IV. The Hairs of Old and Young Ornithorhynchus.

1. Historical, by W. Blaxland Benham, D.Sc. (Lond.), Hon. M.A. (Oxon.), Aldrichian Demonstrator in Comparative Anatomy in the University of Oxford.

The fact that Ornithorhynchus possesses two kinds of hair, larger and smaller, was known to Blumenbach (1) and to Home (2). The latter also recognised the peculiar character of the larger hairs. He writes (p. 69), "The hair is made up of two kinds: a very fine thick fur half of an inch long, and a very uncommon kind of hair three-quarters of an inch long; the portion next to the root has the common appearance, but for a quarter of an inch towards the point it becomes flat, giving it some faint resemblance to very fine feathers." Later, Glockner (3), in a very brief note describes the larger hair in somewhat similar terms. In 1823 van de Hœven (4) reproduced Péron's (5) figures of these hairs; the figures are very small, but are the first published, and show the characteristic flattening, the narrow stalk, and pointed free end.

In his monograph, Meckel (6) makes no addition to our knowledge of these structures.

In 1859 Leydig (7), in his classic paper on the Mammalian coat, is the first to record the fact that the smaller hairs are in bundles—several in each follicular neck—and points out that each hair has nevertheless its own special follicle opening into the bottom of the common pit. He also states that the large spiny hair is surrounded by the bundles of small ones, and he gives a figure (pl. xx, fig. 7) of the arrangement, and shows the sebaceous glands to each hair and the sweat gland accompanying the large one.

These facts are confirmed by Welcker (8), a few years later, who gives measurements of the hairs, the smaller being ·007 mm. in diameter, the larger ones ·045 mm. across. He too

gives a figure (pl. 1, fig. 5) showing the grouping of the hairs, and points out the fact that the roots of the small hairs diverge, that the hairs then converge in the common follicular neck, whence they issue in a bundle (p. 69). Whilst Leydig describes only four or five hairs in a bundle, Welcker found fifteen to thirty of them.

No author gives any histological details of the structure of the hair till Waldeyer (**9**) in 1884, who only describes and illustrates by photographs the difference in the character of the medulla and cortex in the various parts of the larger hair (pl. vii, figs. 100—104). According to him (p. 100), the "bristle hairs" commence basally in a rounded shaft of moderate diameter with a thick medulla; then follows a more flattened but very slender "isthmus," which further on widens out considerably to form the main part of the hair; this narrows again at the tip to a point. The isthmus is non-medullated, and the medulla of the broad part differs from that in the basal shaft. The paper dealing with the skin of Ornithorhynchus, by Souza Fontes (**10**), consists of little but quotations from Leydig. It contains nothing worth recording.

These authors give no information as to the bulb, papilla, and root-sheaths, nor any other histological details of the hair itself.

As to the arrangement of the hair, Meijere (**11**), who has recently examined the arrangement of the hair throughout the Mammalia, gives a figure on p. 49 showing the hairs on the back of Ornithorhynchus in more or less irregular rows—the large hairs, represented as round in section, being separated from each other by three or four bundles of small hairs: on the ventral surface, however, the number of the latter is greater. His measurements closely agree with those given by Welcker, being ·048 mm. diameter for the large ones, ·008 mm. for the small hairs.

1. Blumenbach.—"Anatomical Observations on the Structure of Ornithorhynchus paradoxus," 'Philosoph. Mag.,' xi, 1802, p. 366.
2. Home.—"A Description of the Anatomy of Ornithorhynchus paradoxus," 'Phil. Trans.,' 1802, p. 67.
3. Glockner.—"Ueber die Haare des Ornithorhynchus," 'Isis,' 1819, p. 651.

4. Van de Hœven.—"Mémoire sur le genre Ornithorhynque," 'Nova Acta' (Bonn), 1823.
5. Péron and Lesueur.—'Voyage de découvertes aux Terres australes pendant les années 1800—1804.'
6. Meckel.—'Ornithorhynchi paradoxi descriptio anatomica,' 1826.
7. Leydig.—" Ueber die äusseren Bedeckungen der Säugethiere," 'Arch. f. Mikr. Anat.,' 1859.
8. Welcker.—" Ueber die Entwickelung und der Bau der Haut und der Haare bei Bradypus," 'Abhand. Naturf. Gesell. zu Halle,' ix, 1866.
9. Waldeyer.—'Atlas den Menschlichen und Tierischen Haare,' 1884.
10. Souza Fontes.—'Beit. z. Anat. Kenntniss der Hautdecke des Ornithorhynchus,' Dissert. Inaug., Bonn, 1879.
11. Meijere.—'Over de Haren der Zoogdiere,' Inaug. Dissert., Amsterdam, 1893.

2. General Structure and Arrangement of the Hair.

The hair-like appearance of the epidermic cylinders in the bill led me to investigate the hairs of the body generally, and although the results seem to have no special bearing on the significance of the former structures they are of much value and interest on their own account.

This research was undertaken in the winter of 1887–8, when all the figures (except fig. 24) represented on Pl. 15 were drawn. Since then it has been renewed from time to time, special attention having been devoted to the subject in Professor Lankester's laboratory during the summer of 1892.

Over the general surface of the body and head of Ornithorhynchus we meet with large hairs, each of which is attended by bundles of small hairs. Furthermore, on the dorsal area at least, each large hair is attended by a constant number of four bundles of small ones. The latter commonly vary in number in the dorsal region from seven to twelve in a bundle, and all emerge in a sheaf from a common follicular mouth. The four bundles are arranged on each side of and behind the larger hair, and, as all slope obliquely backwards, the shafts of the small hairs lie beneath that of the large one belonging to the same group.

The protective large hairs are evidently subject to much wear and tear, and succeed each other very rapidly; the new

successional hair, which is to be met with in nearly every section, emerging from the same follicular mouth in front of, and therefore overlapping, the base of the old one. The succession of smaller hairs is less rapid, but one or more younger, growing hairs are to be seen in every bundle. The exact relationship in two instances can be made out by ascertaining the proportion of dark circles (sections of young hairs) to the smaller unpigmented circles (sections of bases of old hairs) in each of the four bundles in figs. 17 and 18 of Pl. 15, which contains all the figures illustrating the structure of the hair of Ornithorhynchus. The proportions in the four bundles of three other groups were as follows:

FIRST GROUP.

Bundle I . . .	1	young hair to	9 or 10	old.
,, II . . .	2	,, hairs to	8	,,
,, III . . .	1	,, hair to	7	,,
,, IV . . .	3	,, hairs to	5	,,

SECOND GROUP.

Bundle I	1	young hair to	8	old.
,, II	2	,, hairs to	8	,,
,, III	1	,, hair to	6	,,
,, IV	3	,, hairs to	7	,,

THIRD GROUP.

Bundle I	2	young hairs to	7	old.
,, II	1	,, hair to	7	,,
,, III	1	,, ,,	8	,,
,, IV	2	,, hairs to	10	,,

The proportion of young hairs was ascertained in each case by counting the numbers of dark and light circles in a section taken sufficiently near the surface of the skin to bring all the hairs of a bundle into a common follicular neck, as in fig. 17. These figures, together with the number shown in fig. 17, prove that, at any rate in the dorsal region, Leydig's estimate of the number of small hairs in a bundle is too small, while that of Welcker is far too large.

Each group of hairs is attended by a single gland exactly

resembling those of the bill of the same animal or the sweat-glands of mammals generally. On the head and back, the duct invariably opens just in front of the large hair, so that it is the most anterior member of the whole group.

Such a group is distinctly represented in transverse section immediately beneath the skin in fig. 17, where the young successional hairs, both large and small, are at once distinguished by the presence of pigment from the colourless bases of the shafts of older hairs. At this level the gland-duct (*d.*) is seen in section in front of the large hair. At a lower level, as shown in fig. 18, the duct is replaced by a secretory tube of typical structure (*g.*), which is often placed, as in this figure, between the large hair and one of the bundles of smaller hairs. The latter, at this level, have become separate, but their outer root-sheaths are continuous peripherally, forming a single epithelial mass. Furthermore, the two masses on each side have approached and tend to coalesce (compare figs. 17 and 18), soon doing so completely. At this level, and just below it, the small unpigmented bases of the older hairs come to an end (one is thus ending in each of the right-hand bundles in fig. 18). The younger growing shafts, with their outer root-sheaths no longer continuous, descend much deeper, gradually converging to form a single bundle, which lies in the middle line under the follicle of the large hair. The growing small hairs then end in bulbs at various levels, but the most deeply placed do not, as a rule, descend so far as the bulb of the large hair.

The large hairs terminate superiorly in large, although narrow, flattened leaf-shaped expansions borne by a shaft long enough to carry them just beyond the ends of the small hairs. As the neck of this shaft is comparatively thin, it is probable that in the living state the terminal shields tend to fall over, and lie flat on the finer hair beneath, their tips pointing backwards and overlapping the basal part of the shields behind them.

The tip of the shield is beautifully formed and free from pigment. Looked at from the side or in section, the pigment

is seen to be more developed on the under side, and a broad unpigmented margin is always found along the upper surface. This is in part due to the cuticle of the upper surface, which is much thicker than that of the under, as can be well seen in sections (fig. 18). The degree to which the pigment extends towards the upper surface differs, however, in individual hairs. Passing along the centre of the shield is a very distinct medulla containing abundant gas-bubbles, entering as a result of the contraction of soft protoplasmic cells, which are present and stain in logwood, &c., in the shields which have not yet appeared above the surface (fig. 18). Traces of this medulla can be followed nearly to the tip of the structure. The pigment is sometimes so far restricted to the under side of the shield as to be entirely beneath the level of the medulla in the middle line, but it extends further at the sides (fig. 18).

Below the shield there is a constricted neck in which the medulla is apparently wanting and the pigment scanty, but immediately below, at the beginning of the long shaft, the medulla is strongly developed suddenly and the pigment assumes the characteristic ladder-like appearance, being arranged in bands alternating with spaces containing colourless shrunken cells and gas bubbles. The arrangement is not, however, so regular as that of the corresponding part of the smaller hairs. Below, the shaft passes into the somewhat more slender unpigmented base in which a medulla is wanting.

Hence in one of the larger hairs we can distinguish a shield, neck, shaft, and base.

The small hairs can be divided into similar regions. The free tip is unpigmented, and is followed by a section corresponding to the shield, with the same longitudinal arrangement of small granules and large fusiform masses of pigment. Traces of a medulla marked by gas bubbles are to be seen in places. Then follows the part which represents the neck,—not, indeed, more slender, but with the same diminution in the amount of pigment and cessation of the medulla. To this succeeds the shaft with an extremely uniform alternation of medullary dark and light bands, the latter containing distinct

gas bubbles. As in the larger hairs, the shaft passes into a pigmentless and, in this case, far more slender base (fig. 18, in which the sections of the colourless bases of small hairs are seen to be much smaller than the dark circles which represent the sections of shafts and upper parts).

There is no trace of either pigment or medulla in the bases of both larger and smaller hairs (see figs. 17 and 18 for sections of bases).

Such is the appearance and arrangement of the groups of large and small hairs which apparently cover the whole surface of the body and head.

On the upper surface of the tail the large hairs become stiff and bristly, but still flattened. They probably correspond to the shields only of the large hairs already described. Passing from the back on to the tail the small hairs become short and scanty, and towards the tip disappear altogether. The successional hair emerges as on the body, and the overlap is the same, but the gland duct opens beneath and behind instead of in front of the hair. The under surface of the tail in a male individual not quite fully grown was covered with short flattened large hairs set very obliquely, in fact almost horizontally. They appear to want the medulla and the hair pigment. In several full-grown individuals this part of the tail was more or less bare, but the bases of large hairs could be detected, together with patches of hairs having frayed and worn ends.

The manus and pes, except for the bare palmar and plantar surfaces, are covered with hairs very similar to those last described, but even shorter.

Everywhere the groups of large and small hairs, or the large hairs alone, appear to be set in irregular rows, transverse to the long axis of the body which they clothe.

3. Comparison between the Hairs of Old and Young Animal.

Very interesting results follow from the comparison of the hairs of the mature animal with those of a young one in which

only the tips of the larger hairs had appeared above the surface, while the smaller ones were still at some distance below it (see Pl. 15A).

The parts of the large hairs which had been formed evidently corresponded to the terminal shields of the adult, from which they differed in their greater thickness, although the differentiation of an upper surface with a greatly thickened cuticle from a lower surface in which the pigment was concentrated, was equally marked (figs. 19, 20, and 23).

The gland, which was quite short in the young animal, opened in front of the large hair, as in the adult.

The small hairs differ from those of the adult and in such a manner as to indicate the probable origin of the four bundles emerging from common mouths.

When longitudinal sections or successive transverse sections of the young skin are examined, each large hair is found to be accompanied by four tubes, exactly like the ducts of glands, opening on the surface. These tubes correspond in position to the four bundles of small hairs in the adult. Tracing them down wards, each tube gives rise to a bundle containing a much smaller number of hairs than in the adult. Each bundle nearly always contains a single hair which is specially prominent, and it is this latter which occupies the lumen of the tube itself, the apex being however, in animals of this stage of growth, a considerable distance below the surface of the skin. In some cases, however, the four bundles of a group appear to contain only three chief hairs between them, in others as many as five or six. Four tubes appear to be always present, evidently representing the four common follicular necks and mouths of the adult. There is great disparity in size between the chief hair in a bundle and the smaller ones which are grouped around it. The hairs of the four sheaves terminate in bulbs, placed, as in the adult, at very different depths below the surface.

From this structure it may be inferred that each of the four bundles is, in the course of development, at first represented by a single hair (the chief one), formed in a follicular

tube which is open to the surface, and that the smaller hairs are developed in follicles which are outgrowths from some part of this open tube, and which do not tend to coalesce as in the mature animal. The distinction between chief and smaller hairs is subsequently lost, probably in the hairs which succeed those described above. In an animal of this age, however, the first-formed hairs have not approached their full size, and no trace of any successional hair—either large or small—is to be seen.

The existence of a distinct lumen opening on the surface at some distance above the apex of the hair is of such great morphological importance and interest in relation to the origin of hairs and their homology with feathers and scales, that the observation was confirmed again and again, by examining both longitudinal and transverse sections, until there could be no doubt about the matter. I was then anxious to ascertain whether the same fact held true with the larger hairs. The general surface of the body was valueless for this inquiry, as the animal was rather too old, and the tips of the large hairs were visible. On the under side of the tail, however, many, at any rate, of the large hairs (here unaccompanied by small ones) had not reached the surface, and there was an open tube above them, as in the case of the small hairs elsewhere. The probable bearing of this and many other peculiarities will be discussed at the end of the paper.

The hairs upon the tail bear the same relation to those on the body as that already described in the adult.

4. Minute Structure and Formation of Hair and its Sheaths.

The hair is developed from a bulb composed, as in other mammals, of polyhedral cells of the rete mucosum connected with the superficial epidermis by an outer root-sheath. Protrusions of the latter give rise to apparently typical sebaceous glands, situated, in the smaller hairs, at the level at which the bundle unites to enter a common follicular neck. The upper

part of the outer root-sheath often contains cystic growths like those described in other mammals.

The bulb is entered by a dermal papilla which is, at any rate in the large hairs of the young animal, of enormous size and length, extending beyond the bulb far into the base of the hair proper, where the cells are fusiform, pigment abundant, and the cuticle well defined (see fig. 23, in which, however, the two halves have fallen apart, so that the hair appears to be thicker than the bulb). The bulbs and papillæ are especially large in the tail.

A very long, well-marked papilla also penetrates the long narrow bulbs of the smaller hairs. The relations of the adult bulb and papilla appeared to be very similar, but were made out with greater difficulty than in the young animal, which was chiefly employed for the histological side of this inquiry.

From the tip of the papilla, at any rate in the larger hairs, an axial rod of soft protoplasmic cells, deeply staining in reagents, is continued (fig. 18, mature; figs. 19 and 24, young). This, when dried and shrivelled, admits the air and forms the characteristic medulla.

Around the papilla the inner zone of cells of the bulb forms the hair proper with its cuticle, the structure and mode of formation being typical except for the bilateral symmetry of the larger hairs indicated by their shape, thickened upper cuticle, and predominant pigment on the under surface (fig. 18, mature; figs. 19, 20, and 23, young).

External to this zone the cells form the inner root-sheath, while the outer root-sheath appears to be continuous with the lower part of the bulb. The latter sheath is probably always typical, but it was extremely hard to make out in certain sections of the young animal (figs. 19, 20, 23), although in others it was perfectly distinct and of normal appearance (figs. 21, 22, 24). This discrepancy is due to the facts that the thickness of the sheath varies greatly at different levels, and that the animal was not prepared for histological investigation.

The inner root-sheath is always present in the developing hair, and is a structure of great importance, throwing much

light upon the corresponding sheath as it is described in other mammals. As in the latter, the inner root-sheath surrounds that part of the hair which is enclosed in the follicle, but growing less rapidly it does not extend to the neck through which the hair protrudes; hence we do not find it at all in sections of the upper part of the follicle (figs. 17 and 18). It is far thicker and more important in the hairs of the young animal, and especially in those of the tail (figs. 21 and 22, *i. r. s.*). In structure it consists of a network of corneous fibres enclosing fusiform meshes with a longitudinal direction, through which the outer root-sheath can be seen (fig. 24). Hence in certain cases Henle's original description of his inner root-sheath as a fenestrated membrane is certainly true of Ornithorhynchus. Henle's account is also followed by Mertsching ('Archiv f. Mikr. Anat.,' 1888, p. 32), who shows in pl. v, fig. 8, that this sheath in the human hair possesses a fenestrated structure. In transverse section the corneous fibres of Ornithorhynchus are seen to be polyhedral and irregular in outline (figs. 19, 21, 22, *i. r. s.*), and if the section be taken at some little distance above the bulb, distinct spaces appear between them (figs. 19 and 21). Round the small hairs, on the other hand, only a uniform layer of the proportions usually found in Mammalia could be detected (fig. 19). In some of the longitudinal sections of larger hairs I could make out a thin internal layer exhibiting a serrated edge, with teeth the reverse of those on the hair cuticle. This evidently represents the so-called cuticle of the inner root-sheath, and it is probably shown in section in fig. 21. Well above the bulb (fig. 21) this thin internal lamina was the only trace of a separation of the sheath into layers, and even this could be detected only occasionally; and I gained the impression that it is not a distinct and definite layer, but merely the condensation, as it were, of the innermost part of the inner root-sheath upon the exterior of the hair and the moulding of its surface by contact with the cuticle of the latter. But at a lower level, just above the bulb, there is seen what I believe to be the homologue of Huxley's and Henle's layers. Thus in fig. 22 the fibres of the inner zone have not become corneous and take the stain readily,

while still nearer the bulb in fig. 20 the same inner layer shows distinct traces of cells with their nuclei. In both cases this inner zone probably represents Huxley's layer, but it does not, at least in Ornithorhynchus, imply any differentiation of the sheath into layers, and when we consider the immense development of the structure in this animal, it seems probable that the distinction can hardly be sustained throughout mammals generally. The appearance which has led to the separation of the sheath into two layers is, I believe, due to the fact that the inner and outer zones do not arise from the cells of the bulb at one and the same horizon, but that the inner zone rises at a higher level than the outer. It therefore follows that, in sections at a certain horizon, the cells of the bulb will have undergone complete transformation into the corneous substance of the sheath in the outer zone, while they will still remain unchanged, and at a rather higher level only partially changed, in the inner zone. At any rate, I am convinced that this is the explanation of the two layers in figs. 20 and 22.

In certain sections the inner part of the sheath appears to be made up of fibres and the outer part homogeneous (fig. 18), but in the thickest and best developed sheaths (fig. 21) the fibrous structure is distinct in the outer as well as the inner part (with the exception of the thin "cuticle").

5. Mode of Succession of the Hairs.

The succession of the hairs already alluded to presents some features of great interest. The appearance of two hairs in one follicle is spoken of as an occasional appearance in other mammals. In the large hairs of Ornithorhynchus it is the invariable rule, and the succession follows the bilateral symmetry of the hair itself, the new hair always overlapping the anterior surface of the old. Hence a section of the neck of the follicle commonly shows the terminal shield of the emerging young hair anteriorly, and the circular or oval base of the old hair opposite the middle of its posterior surface (fig. 17). We do not find two shafts in one neck, because the old hair is doubtless shed by the time that the new shield has risen above the surface.

In deeper sections it is found that the base of the old hair, becoming irregular in outline, first enters (fig. 18), and then soon comes to an end, in the posterior wall of the outer root-sheath, terminating as a knob, a rounded end, or in diverging lines of corneous cells, which spread among the cells of the sheath; while the new hair passes far deeper and ends in a bulb. When, similarly, successively deeper sections of a bundle of small hairs are examined, it is found that the pigmentless bases of old hairs soon come to an end, together with their follicles, while the much larger coloured shafts of the still growing hairs pass down far deeper to end in bulbs. These appearances are confirmed by the examination of longitudinal sections, which show that the extreme ends of the bases thin away, become sinuous, and sometimes branch among the cells of the outer root-sheath.

The probable interpretation is as follows:—All the parts of a hair which possess the typical structure are developed from a bulb, which is nearly exhausted when the hair has almost attained its full length. The hair is, however, further protruded by the development and growth of a solid and pigmentless base possessing none of the typical features of a hair, from the outer root-sheath, which is thus used up, the whole follicle being shortened and retracted towards the surface. When the base of the old hair has reached a certain height the lower blind end of the outer root-sheath begins to descend again, forms a new bulb and a new hair, which therefore ascends and passes the base of the old one. It is perhaps significant that each fresh hair which develops during the life of the individual should originate in an epidermic downgrowth, thus repeating the development of the first-formed embryonic hair.

It is, I think, improbable that the outer root-sheath which forms the base of the old hair, and not the typical structure of the shaft, should itself possess the power of originating a new bulb. It is more probable that the new bulb is developed from cells which are the genetic descendants of the old one, and which retain similar potentialities.

In the case of the small hairs, however, we do not meet with two in any of the single follicles; and here the old hair is shed before the tip of the new one reaches its base, or, as I think more probable, a new follicle is formed, perhaps from the point which represents that at which the earliest follicles were budded out from the first single tube.

6. Recapitulation of Essential Peculiarities of Hair of Ornithorhynchus as compared with that of Higher Mammalia.

In order to draw the conclusions which, as I believe, follow from the investigation of these structures in the lowest mammal, it will be convenient to recapitulate, making a short statement of the points in which the hairs differ from those of other Mammalia.

In the GROUPS OF HAIRS we notice a marked bilateral symmetry (fig. 17), and a definite relation to the bilateral symmetry of the body itself.

In the LARGE HAIRS there is (1) a most distinct bilateral symmetry in shape, in structure (differentiation of upper and lower surface), and in succession, and a definite relationship to the bilateral symmetry of the body. The terminal shields are scale-like, especially in the tail, where they become sessile.

(2) The inner root-sheath is of immense size (especially in the tail), and possesses a definite and peculiar structure, being formed of longitudinal corneous fibres united into a network.

(3) The bulb and papilla are extremely large, the latter penetrating the base of the hair.

(4) The hair is developed in a tube, which is open to the surface,—in a tubular and not a solid downgrowth from the epidermis.

The SMALL HAIRS are (1) arranged in bundles, which are bilaterally disposed in relation to the large hair, and have a definite relationship to the bilateral symmetry of the body, although the shape and structure of the individual hairs is not

bilaterally but radially symmetrical, while the succession is probably asymmetrical. In these characters and in the general appearance the individual smaller hairs are not scale-like, but resemble those of Mammalia generally.

(2) The inner root-sheath has about the same relative size and the same appearance as that of Mammalia generally.

(3) The bulb and papilla are both very long and narrow, but apparently not so remarkable as those of the large hairs.

(4) The hair is developed in a tube open to the surface.

(5) The fact that the bundles of small hairs reach the surface by a common follicular mouth is probably shown by the mode of development to be a comparatively recent feature of no ancestral significance.

Comparing these features of the large and small hairs, we may omit the last-mentioned characteristic of the latter, which is probably unimportant. There is similarity in the most important point of all—development in open tubes; but in every other respect there is divergence, and always of such a kind as to bring the small hairs nearer to those of mammals generally. Furthermore, the characters which separate the large hairs from those of other mammals are, as I hope to show in all cases, characters which suggest homology with one or other of the epidermal structures of the higher Vertebrate Classes.

V. The Homologies and Origin of Mammalian Hair.

1. Historical; by W. Blaxland Benham, D.Sc., &c.

There are two main suggestions as to the relation of hairs to other Vertebrate epidermal structures:

(1) The first is that hairs are homologous with the scales of reptiles and the feathers of birds.

(2) The second regards them as not homologous with these structures.

In the latter case two other epidermal structures have been suggested as the ancestors of hairs:—(*a*) Maurer would derive hairs from epidermal sense-organs of fishes and Amphibia; (*b*)

Emery regards hairs as "substitution-derivatives" of certain elements of the placoid scales of fishes; whilst (*c*), finally, there are authors who have contented themselves with contesting the hair-feather-scale theory, but have not attempted to homologise hairs with anything else, appearing to regard them as structures sui generis.

All authorities appear to be in agreement that scales and feathers are homologous structures. The mode of origin is closely similar in the two cases—the first forecast being an upgrowth of the corium giving rise to a papilliform projection carrying the epidermis outwards; the cells of the epidermis then proliferate to a slight extent, and later become horny. In the scale the papilla is more or less flattened, with its free edge (apex) directed backwards, and the cornification becomes more marked on the upper (outer) surface than on the lower (inner) surface of the papilla.[1] In the case of the feather, the papilla becomes more or less cylindrical and more upright; further, its base sinks down into the corium at an early age, so that the root of the feather comes to lie in a follicle. The axis of the papilla (corium) gives rise to the pith of the feather axis; the enveloping cornified epidermis to the barbs. But the most superficial coat of the papilla (the original outermost layer of epidermis) forms a sheath which closely surrounds the feather forecast. As the latter grows it breaks through the apex of the sheath, which then dwindles and is ultimately cast off. This feather-sheath consists of two layers of cells—a more superficial cornified layer, and a deeper layer of granular cells.

The feather, then, may be derived from a scale by supposing that the original papilla, after growing outwards for a time, has sunk downwards into the corium so as to give rise to a follicle and a root-sheath, for the purpose of better support and nutrition.

Those authors who take the view that the hair is homologous with the feather, believe that this process of sinking has gone

[1] It is noteworthy that this statement is in every detail an exact description of the formation of the large hairs of Ornithorhynchus, save that they are developed as an upgrowth at the bottom of an open pit.—E. B. P.

on further, and that it takes place at an earlier stage in the ontogeny of the hair; while the proliferation of the epidermis also commences much earlier than in the feather-forecast, and is more extensive and rapid.

On the other hand, it is argued that if the hair is homologous with the feather, there should be a more or less close agreement in (*a*) the final structure of the two, (*b*) their mode of development, and (*c*) their arrangement on the body. It is unnecessary here to compare the structure of hair and feather in detail. In both there is a (1) root (embedded in the skin) embracing a vascular papilla, which is of much greater extent in a feather than in a hair; and (2) a projecting shaft of horny cells (which in the feather is flattened like a scale, but bears secondary processes upon it, while in the hair it is cylindrical or flattened). With regard to the arrangement of these structures, nothing need, I think, be said here. But in dealing with the development we are at once met with the fact that two divergent accounts have been given with regard to the very first forecast of the hair. Some authors, amongst them Götte (2), Reissner (1), Studer (4), Kerbert (3), describe the first trace of a hair as showing itself in the form of a projection of the corium into the epidermis, just as in the feather and scale. This is the view which is taken by all those who regard feathers and hairs as homologous (Claus, Wiederheim, Hertwig, and others).

It may be well to refer to the observations of Davies (5) on this point, who finds the earliest forecast of a hair—or rather a spine, for he studied the matter in the hedgehog—marked out by a proliferation of "intermediate cells," and not by the deeper columnar cells. He carefully describes the mode of origin of feather and spine, and regards both of them as descendants from a common scale-like structure. He holds that the "scales" covering the feet of birds are not homologous with Reptilian scales; the former frequently carry feathers, just as the "scales" of Dasypus carry hairs, and he argues that if the reptilian scale is equivalent to a feather and to a hair, then two of these homologues cannot be superposed. These scales

in birds are merely secondary thickenings round the base of the feather.

He compares the hair rather with the definitive feather, which arises from the root of the down papilla, and he emphasises the fact that in this case, as in the hair, the feather forecast has to make its way up through the neck of a solid follicle of degenerating cells (cf. his figs. 30—39), as on the appearance of the definitive feathers there has been an active downgrowth of the primary feather follicle.

The spine of the hedgehog is, of course, derived from a more simple hair, and is not to be compared with the quill of a feather.

On p. 629 he summarises his ideas on the mode of origin of the feather:—1. A simple thickening of the skin. 2. A radially symmetrical knob. 3. A backwardly directed papilla whose horny layers become thickened round the apex. 4. A backwardly directed papilla whose point ended in a short, thick, hair-like process. 5. A longer hair-like structure, which consisted of a firmer cortical layer and a looser axial tissue, and whose base became sunken with the cutis papilla into the skin. 6. By the bursting of the wall of the freely projecting part of this structure the enclosed tissue became free, and, separating into distinct filaments, gave rise to the primitive "down."

But even admitting the general similarity in the mode of their development, one of the earliest to draw attention to the striking difference between hairs and feathers was Gegenbaur, who contrasted the early outgrowth of the feather forecast, in which the greatest share is taken by the corium papilla, with the early downgrowth of the hair forecast, due to active proliferation of the epidermic constituents.

This doubt as to the strict homology of feather and hair is accentuated by the statements made by other observers—Kölliker, Romer (12), Maurer (9), &c.—that the corium papilla is not the first to become defined, but that the epidermis is for some time the only representative in the hair forecast. This statement, which appears from Maurer's work (1892) to hold true for a variety of forms, may be explained in either of two ways:

the upholders of the hair-feather homology interpret it merely as a precocious development of the epidermic constituent, owing to the greater importance of the root in the hair, while the corium papilla, which only becomes of importance for nutritive purposes at a later stage of development, is correspondingly delayed. Such blearing of the record is not unknown in ontogeny; indeed, the fact that the follicle of the hair commences as a solid structure with no morphological communication with the exterior, and only later shows a differentiation into outer and inner root-sheaths as the hair pushes its way through the superficial layers of epidermis may be, and has been, explained by invoking the same causes—precocious and retarded development.

But another meaning has recently been given to the early activity of the epidermis in the formation of the hair. This and the various other divergences from the process occurring in feather-formation have been regarded as pointing to an entirely different ancestor for the hair, viz. to the epidermal sense-organs of fishes and Amphibia. Maurer (1892) is the parent of this ingenious theory, and discusses the question in a very complete and thorough manner. In his earliest paper he contrasts the development of hair, on the one side, with that of the feather and scale on the other. He has examined the matter for himself, and finds what he regards as very essential differences between them.

He describes the early stages in the development of the hair in a variety of mammals,—cat, mouse, mole, hedgehog, *Dasyurus*, and *Perameles*; and though the details may differ, he finds that invariably the first trace of a hair is expressed by the elongation of the cells of the *deepest layer* of the epidermis; so that the forecast is sharply marked off from the surrounding epidermis. These elongated cells may, as in *Talpa*, reach the surface, which is here slightly pitted (giving an appearance exceedingly similar to that of an early stage of an Ichthyopsid sense-organ). Usually, however, the superficial flattened cells of the epidermis are continued over the tops of the elongated cells. The modification of cells indicating a corium papilla

appears distinctly later—in Dasyurus very much later. Papillæ of the corium are scattered about, in many of the cases studied, quite independently of hair forecasts; and Maurer believes that these papillæ, even if they happen to underlie such forecasts, are not the true root papillæ of hairs.

In the development of feather (or scale) he finds very marked differences; the papillæ—projections of corium—are distinctly the first to appear, and the epidermis covering a papilla is for a considerable time not different from the surrounding epidermis. There is no elongation of cells of the Malpighian layer; the deepest cells are cubical, as elsewhere. The papilla, it is well known, as it grows outwards becomes oblique, so that upper (outer) and lower (inner) surfaces are distinguishable; the epidermis is scarcely changed, but is thicker on the outer side, and this thickening is due to proliferation of cells in the middle layers—not of the deepest layers. With regard to the root-sheath of a hair,—suppose, he says (1893, *b*), that an epidermic scale or feather, with its papilla, were to sink downwards into the corium (as a hair forecast does) then the resulting sheath will be simple. A deep-lying position does not necessitate a complex sheath enclosing the horny structures; so that an epidermal structure, borne by a deep-lying papilla and possessing a complex sheath (hair), is not directly explained as a papilla which has sunk downwards (feather). Further, although the feather-sheath is fairly complex, it is very early cast off after the feather forecast has ruptured the apex of it; whereas the root-sheath of a hair persists throughout life and grows so long as the hair continues to grow. He gives (1893, *c*) an explanation of this feather-sheath—he compares it with the moulted cuticle of reptiles. In the case of these animals, more or less extensive portions of the stratum corneum are from time to time cast off; but before this occurs the underlying epidermis has formed a new "cuticle" and new stratum corneum, so that in section the old stratum corneum does not rest directly upon the new one, but is separated from it by a layer of granule-containing cells; below this is the new "cuticle" and then the new stratum corneum. The feather-sheath consists of an

outer layer of cornified cells and a deeper layer of granule-containing cells, immediately surrounding the feather forecast. This sheath, then, that is shed later on, he believes to be the same thing as the old "cuticle;"—instead of a new "cuticle" below it, there has been formed the feather. He thus explains this feather-sheath in much the same way as the believers in the feather-hair theory might explain the inner root-sheath. But, he points out, there is no such periodical shedding of the stratum corneum in mammals, preceded by the formation of definite layers below; there is a gradual transition from the deepest layer to the most superficial cells which drop off from time to time.

Having in this way contested the supposed homology between hair and feather, he proceeds to elaborate his theory as to the homology between a hair and an epidermal sense-organ of fish and Amphibia. He believes that there is no essential difference between an "Endknospe" and a "Nervenhügel;" each is essentially a collection of nerve end-cells (which may or may not traverse the whole depth of the epidermis) surrounded by elongate supporting cells, which separate the organ from the general epidermis. He describes (1892, *a*) these in various fish from different parts of the body. In the Perennibranchiate Amphibia and in several Caducibranchiate (e. g. Triton) they exist throughout life; while in others (Salamandra) and in Anura they are present only in the larva.

In the newt, after the metamorphosis, these sense-organs have a definite relationship to the wart-like papillæ which have made their appearance. At the top of the wart, in a cup-like depression, lies the sense-organ, which is protected by the overhanging lips of the cup, formed of horny epidermal cells. This removal of the sense-organ from the surface and its loss of function are evidently related to terrestrial life, and differ from the sinking of this same organ in fishes, where it still retains its function.

In Menopoma, Menobranchus, and Cryptobranchus, though aquatic, the sense-organ is similarly removed from the surface; this he explains by the suggestion that these

forms were originally terrestrial and have returned to an aquatic life. Now in Cryptobranchus the condition of the sense-organ and its relations are very interesting. The epidermis contains a considerable number of layers, the three or four outer ones being horny. The sense-organ at the apex of the wart-like papillæ is oblique to the surface; there is a corium papilla below it, on the apex of which the sense-cells are grouped. The supporting cells are greatly increased in number, and leave only a very narrow channel between them leading to the centrally-placed sense-cells.

After describing these organs, he proceeds to compare the various parts with those of a hair. The axially-placed sense-cells, having no longer any purpose to serve, have disappeared, and with them the nerve; nevertheless, the cells are represented by the medulla of the hair. The supporting cells have given rise to the cortex; the outermost, or covering cells, as he terms them, become the cuticle, while the protecting cells, overhanging the sense-organ in Triton, &c., are represented by the inner root-sheath in the hair. This gives what in Maurer's opinion is the only intelligible explanation of this inner root-sheath.

In reply to this theory as to the origin of the Mammalian hair, Leydig (8) admits that there is no doubt a remarkable similarity in the mode of development of the two structures, but points out other structures which might with greater probability be taken into consideration in dealing with its phylogeny, viz. the "perle-organe" of certain Cyprinoid fishes and the "femoral glands" of Lizards, which he had previously described (7). He rejects a view which he was tempted at one time to hold, that hairs may be derived from horny projecting papillæ on the skin of Amphibia which are mere local thickenings of the epidermis. Maurer again (*c*) takes up the cudgels in favour of his theory, and describes the results of his own examination of these two organs, which he has made with an open mind, putting himself, as it were, in the position of a sceptic of his own theory. But he finds no reason to alter his previous opinion, indeed is strengthened in it: he adduces confirmatory evi-

dence and launches other arguments against the feather-hair theory.

Still more recently, Emery (15) has given in a preliminary note another view as to the origin of hair, promising further details later. Hairs are not homologous with scales and feathers, but all three are descended from the placoid scales of fishes by the substitution of horny material for bony substance. In other words, the horny part of these structures in the higher animals represents the enamel, and the underlying papilla (whether ossified or not) represents the basal (cement) plate of the placoid scale. Starting with this assumption, for which he at present brings forward no justification, he seeks to show that he is supported by the relation of the hairs to the scales in the scale-bearing mammals, for he finds, as did Romer for Dasypus, that hairs arise on the papillæ or forecasts of scales, and not between them, as Weber believes. In cases where hairs are, in the adult, situated between scales (as on parts of the body of Dasypus, Chlamydophorus, and other mammals) Emery supposes that the scales which originally bore the hairs have been crowded out of existence by the greater development of neighbouring scales, which in their turn may lose the hairs; these, however, may commence to develop, as Romer has shown in the case of Dasypus.

With reference to the "scales" of certain mammals (Manis, Dasypus) it has been stated, though without sufficient foundation, that they are "fusions of hairs." There is, however, not the slightest foundation for this view, as Max Weber (13), Romer (12), and others have pointed out. They are true scales, similar to those of reptiles[1] and having a similar developmental history, the chief difference being the shedding of the scale in reptiles and its permanence in mammals. Both the above-mentioned writers agree in regarding the scales and hairs as different structures. Thus Romer says, "Hairs have nothing whatever to do with scales;" whilst Weber, in a later paper (14), hesitates to adopt either Maurer's view or the earlier theory. Weber, however, regards the scales of Manis, those on the tail

[1] Davies, however, denies this.

of the rat and other mammals, as directly descended from those of reptiles, and as remnants of an original scaly covering of mammals; the arrangement of hair on the body of these animals being dependent upon the scales. He also holds that even in scaleless mammals the arrangement of hair retains the impress of the original scaly covering. Romer, on the other hand, regards the scales as secondarily acquired. These scaly mammals are, according to him, descended from hairy mammals; the epidermis merely retains the power, inherited from reptiles, of forming scales, which are thus not directly descended from those of reptiles and not strictly homologous with them (rather they are homoplastic).

As to hairs, Romer does not attempt to refer to any other epidermal structure as their ancestor, but follows Haacke in his suggestion that an explanation of the epidermic downgrowth of the hair forecast may be found in the fact that the scales of reptiles touch or overlap, and between two scales there is therefore a depression of the epidermis. Of this he says, "In this epidermal depression I see the spot for the origin of the hair, whence the hairs will develop by a cornification of the epithelial cells."

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15. Emery.—"Ueber die Verhältnisse d. Säugethierehaare zu Schuppenartigen Hautgebilden," 'Anat. Anz.,' viii, 1893, p. 731.

2. Conclusions derived from the Study of Ornithorhynchus.

Referring to the interesting historical account written by Dr. Benham, I will first endeavour to give reasons which seem to me to oppose Gegenbaur's and Kölliker's distinction between hairs on the one hand and feathers and scales on the other, founded on the fact that the former are developed from the base of a solid epithelial downgrowth, the latter from an epithelial upgrowth.

I have never regarded this distinction as a very important one, and I believe that it may be successfully opposed even if we had not the arguments which follow from the condition here shown to obtain in Ornithorhynchus. The papilla and epidermic bulb forming the hair are clearly parallel to the papilla and epidermic cells over it forming the feather and scale, the one projecting upwards at the bottom of a solid downgrowth, the other projecting upwards from the free surface. The only morphological distinction worthy of consideration is the fact that the downgrowth is solid. But even this difference is, in all probability, to be explained as a simple result of the formation of follicle first and hair afterwards as contrasted with feather first and follicle afterwards, while the reversal of order is not in itself at all difficult to understand.

If the cells of the bulb were to form the merest trace of a hair at the surface, and were then carried down in the sinking follicle, the hair rudiment descending in the axis would necessarily leave a lumen behind it—an open tube connected with the surface. If such were the case there would be no morphological distinction between hair and feather, for the follicular downgrowth would still be secondary in the hair as it is in the feather, although preceding the development of everything except the hair tip. And such a hair, developed, except for its tip, from an epithelial upgrowth rising from the bottom of an open tube connected with the surface, would still be, from a morphological standpoint, at the surface, and would be entirely and strictly homologous with a structure developed from an epithelial upgrowth rising from the surface.

This will be admitted, and yet the transition from such a condition to that now met with in Mammalia generally is so easy that no important morphological distinction can be founded on it. It is merely that the same tendency which has gradually increased the relative proportion of development at the bottom of the tube carries this process one small step further, so that the whole hair is formed beneath the surface. There would then no longer be such a slight upgrowth from the bottom of the sinking tube as would ensure a free lumen, and sooner or later a shorter simpler method, leading to a solid downgrowth, would replace the open follicle. But all this does not imply any great morphological distinction. The case is, in fact, exactly parallel to the development of a gland—which at an earlier stage was produced from a tubular depression of the surface—from a solid downgrowth which subsequently becomes tubular; and the chief principle at work would probably be the same in both cases, viz. the tendency towards abbreviation and simplification of development.

As a confirmation and a test of this argument it is important to inquire whether the solid cylinder above the primitive bulb forms any part of the hair itself, or whether it gives rise only to the epidermic walls of the follicular tube (outer root-sheath) which is afterwards formed. If the solid cylinder represents

an abbreviated development of the epidermic tube, we should expect its constituents to be histologically equivalent to those of the tube, and of nothing else.

Different writers have taken different sides upon this question, some accepting such an account as that summarised by F. Balfour,[1] following Kölliker,[2] that the hair develops as "a cornification of the cells of the axis of one of the . . . [downgrowing, solid, epidermic] processes, and is invested by a sheath similarly formed from the more superficial epidermic cells;" and that given by Gegenbaur[3]—"the shaft is differentiated from the invaginated epidermis by the cornification of its cells, while the other cellular parts of the follicle form the root-sheaths." The other point of view is concisely expressed by Klein,[4] who describes the hair and inner root-sheath as formed by the bulb alone, and pushed up the axis of the solid cylinder of cells which connects the bulb with the superficial epidermis, and who expressly states that "the cells of the primary solid cylinder represent the rudiment of the cells of the outer root-sheath only."

The latter account is supported by the fact that, as soon as the tubular follicle has been formed, it possesses no power of development into a hair. This power is only present in the epidermic upgrowth from the bottom of the tube, which represents, on the view expressed above, the epidermic upgrowth at the surface from which the primitive hair was developed. The walls of the tube, the outer root-sheath, have no such power, but, as has been previously pointed out, can only form the far less complex structure of the hair-base.

In the case of successional hairs some authorities consider that the new bulb is formed from the outer root-sheath of the old, while others regard it as formed from the old bulb. Even on the former hypothesis there is no difficulty in looking upon

[1] 'Comparative Embryology,' London, 1881, vol. ii, p. 328.

[2] 'Entwickelungsgeschichte d. Mensch. u. der höheren Thiere,' Leipzig, 1879.

[3] 'Comparative Anatomy,' translation by Bell, London, 1878, p. 420.

[4] 'Atlas of Histology,' London, 1880, p. 325.

it as formed from some cells of the old bulb which have not been used up in forming the old hair, and which have followed the shortening tube.

I therefore believe that, accepting Gegenbaur's account of the development of a hair, the most probable interpretation is still to regard it as morphologically equivalent to a scale or feather.

When, however, we study this development in the very direction from which most help is to be expected, and ascertain the process which takes place in the most ancestral mammal, there can surely be no doubt about the matter. For the solid downgrowth of the higher mammals is replaced by an open tube in Ornithorhynchus. To an evolutionist this fact cannot fail to be the clear demonstration that the solid cylinder is the abbreviated representative of the open tube. With this fact, the significance of Gegenbaur's distinction between feather and hair falls to the ground.

It is, indeed, by no means improbable that the first and earliest trace of the hair is formed at the surface in Ornithorhynchus, and subsequently sinks with the deepening tube. Material by which this suggestion could be tested is unfortunately wanting.

But the open tube is not the only, although it is the most, important point about the development of the hair of Ornithorhynchus. The great length of the papilla projecting through the bulb into the lower part of the hair is also very significant, suggesting a previous development like that of a scale or feather from the surface of the epidermic covering of a papillary core traversing the structure from base to apex.

Further confirmation is afforded by the axial rod of soft protoplasmic cells forming the medulla of hair; for a shortening papillary core, surrounded by cells of the rete mucosum superficially undergoing cornification, would tend to leave just such an indication of its former presence.

This interpretation is strongly confirmed by the beautiful and detailed figures of A. Mertsching ('Beiträge zur Histologie des Haares und Haarbalges,' 'Archiv fur mikrosk. Anatomie,' 1888, p. 32). Thus in pl. iv, fig. 1, he shows in human hair,

and in pl. v, fig. 4, still better in that of the guinea-pig, that the papilla terminates superiorly in a long slender process, which becomes actually continuous with the interspaces between the medullary cells, while the latter cells cover the lower part of the process as a single layer and are represented as continuous with the lowest layer of columnar cells covering the papilla in the region of the bulb. Until we reach the region where the medullary cells have shrunk and degenerated, the apex of the papilla is represented as forming an axial tube in the base of the hair, and the medulla as its epithelial covering in the form of a single layer corresponding to the lowest layer of the epidermis.

The gradual increase in relative length and diminution in diameter brought about by the necessity for warmth, have implied solidity of structure, while firmness of attachment has demanded the follicular invagination. Development at the bottom of the follicle, together with the changes in shape, have led to the present condition in which the structure is formed from the lower end instead of from the surface of a cylinder, the axial traces of rete remaining as a vestige of the past.

Turning to more recent work, we find that Maurer seeks to establish a distinction between hairs and scales or feathers, in the elongation of the lowest epidermic cells which precedes the development of the former but not the latter. But he has never made this observation upon a Monotreme, and until this has been accomplished no very great weight can be attached to his argument. Indeed, the results which I have obtained afford grounds for the belief that the earliest stages of development will approach those of scales and feathers far more closely than is the case with the higher mammals.

Some of the features especially pointed to by Maurer as characteristic of feathers as opposed to hairs, are equally characteristic of the hairs of Ornithorhynchus. Thus, both in obliquity of direction and in distinction between an upper and a lower surface, the large hairs of Ornithorhynchus resemble feathers.

I entirely agree with Maurer that any explanation of the hair which fails to account for the inner root-sheath is a failure; but I hope to show that a reasonable explanation is quite possible on the hypothesis that hairs and feathers are homologous. Indeed, when Maurer comes to criticise the parallel between a hair and a feather sunken in a follicle, I wonder that the homology between inner root-sheath and the appendicular parts of a feather did not suggest itself to him. Had he seen the strongly developed thick fibrous sheath of Ornithorhynchus, I venture to think that he might have come to a different conclusion.

The true significance of any peculiar structure in the higher members of a Class is to be best understood by the study of those lower forms in which its undoubted homologue is far more strongly developed. If we only knew of the hairs of the higher mammals, there would be a great deal to be said for Maurer's theory. But it fails because it is framed to account for the Mammalian hair as it is, and not to account for it as the condition in Ornithorhynchus shows that it has been. Thus, his explanation of the inner root-sheath may fairly account for the structure as it is usually described, but it fails to account for it in the lowest mammal. Again, he explains hair as a radially symmetrical structure, but Ornithorhynchus shows that it is primitively bilateral. The same objection may be raised to his explanation of papilla and solid epidermic downgrowth; the explanations do not apply to Ornithorhynchus.

As to his objection that mammals have nothing comparable to the moulting of scales in reptiles, it may be replied that the succession of hairs affords as close a parallel as the mechanical conditions of the case admit. Replace the flattened scale growing from its under surface by the solid slender cylindrical hair growing from its lower end alone, and it becomes clear that the flaking off of the corneous surface of the one can only be paralleled by the loss of the whole corneous cylinder of the other and its replacement by a fresh one. Furthermore, the new large hair is, in Ornithorhynchus, far advanced in development before the old one is shed. Hence there is exactly what

Maurer denies to mammals—a periodical shedding of the stratum corneum (hair) preceded by the formation of a new stratum corneum (new hair) below. The succession of hairs is, in fact, the one exception to the gradual wearing off of the superficial corneal cells in mammals which is so important a difference between them and reptiles.

Although quite accepting Max Weber's explanation of the scales of Manis, I should agree with Romer in thinking it more probable that they are homoplastic rather than homogenic with reptilian scales. We must remember that the tongue of mammals possesses in its papillæ structures quite as comparable, except as to situation, with the scales of reptiles as are those of Manis; while protection, attrition, or any other advantage which can be secured by a papilliform upgrowth from the surface, is obtained so simply that it seems unnecessary to explain it by genetic relationship.

My objection chiefly turns, however, on the conclusions forced upon me by the study of Ornithorhynchus; for if hairs are modified scales and homologues of feathers, it is very unlikely that the scales of Manis can be the same. Romer and Emery both show hairs developing on the scales of Dasypus, while they also prove that these scales are homologous with those of Manis.

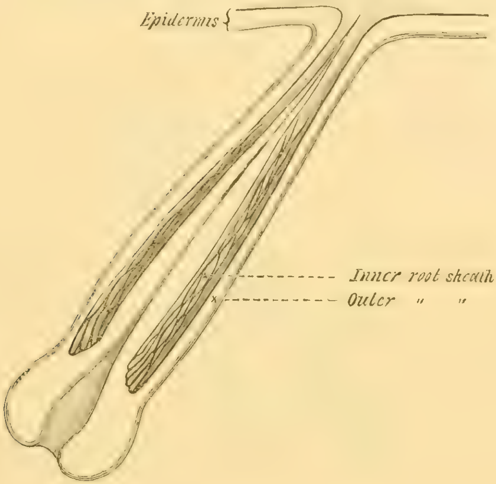
Both feather and hair point to some ancestral scale which is very different from that now found in reptiles and in Manis. I believe that some of the features of this primitive structure can be reconstructed with a fair degree of probability.

Inasmuch as I have argued that the hair of Ornithorhynchus, developed in an open pit, was in some ancestral phase formed upon the surface, it is legitimate to regard it as a superficially placed structure, and then to inquire whether new homologies or discrepancies between it and feathers or scales, are thus revealed.

Woodcut fig. 1 is a diagrammatic rendering of a longitudinal section of the developing shield of a large hair in Ornithorhynchus, while woodcut fig. 2 represents its appearance if it were formed at the surface instead of in a pit. The wall of the pit,

the outer root-sheath, has of course disappeared, while the inner root-sheath forms a thick fibrous network round the base of the hair. No longer confined in the narrow space between hair and outer sheath, its fibres would be looser and their free ends would curl up.

FIG. 1.

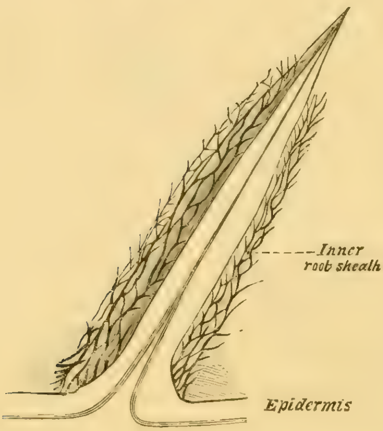


Giovanni has recently ("De la regeneration des poils après l'épilation," 'Archiv f. mikr. Anat.,' 1890, p. 528) published most beautiful illustrations of the earliest phases and growth of the successional hair in man. He shows in pl. xxv, figs. 13, 19, 25, that the tip of the inner root-sheath is the first product of the bulb, and that the hair itself is formed later and pierces it (pl. xxvii, figs. 1, 6, 11). The appearance suggests a possible homology of inner root-sheath with the sheath of a developing feather, but the specialised character and great size of the former in Ornithorhynchus favour rather the homology with the appendicular parts. The growth of the inner root-sheath round the base of the hair is to be explained by the shortening of the cone round which both the primitive hair and sheath are here supposed to have developed. The final result of such shortening leaves the hair to develop in the axis and the sheath

round its periphery. Giovanni's account is important in this relation, proving that the inner root-sheath is at first formed over the apex of the future hair, and only assumes its normal relationship when the hair has grown through it.

We have in woodcut fig. 2 the representation not only of the expanded tips of the larger hairs of Ornithorhynchus as they would be if they grew at the surface, but of flattened

Fig. 2.



imbricated protective scales with a rich fibrous growth round their bases and sides, a growth which in the form of a thick continuous felted under-coat would be of the greatest assistance in maintaining a constant temperature.

By far the most bird-like structures in Archæopteryx, as we know it, are its feathers. While its skeleton is profoundly modified from that of the typical bird, its feathers remain entirely typical.

Among the most Mammalian structures in Ornithorhynchus are its hairs, and although they differ in some important respects from those of other mammals, their divergence is small compared with that of development, ovary, skeleton, &c.

This extraordinary persistence of the epidermic characters of the Class when other Class characters are failing, suggests most strongly a persistence altogether beyond the limits of the Class.

We are thus led to believe that both feathers and hairs were, so far as their essential structure is concerned, existent in the Reptilian ancestors of birds and mammals.

Now in woodcut fig. 2 we have the representation of a scale which contains everything essential to the structure of both hair and feather—equally capable of attaining, and attaining by no very important changes, the simplicity of the one and the complexity of the other.

On this hypothesis the hair represents the axial, its inner root-sheath the appendicular part of a feather; and thus an intelligible morphological significance is given to the mysterious inner root-sheath—a true part of the hair itself, and with it arising from the bulb—but which, owing to the mode of development, is buried deeply beneath the surface.

It is, indeed, possible that the existence of such a thick under-coat may have conferred upon the ancestors of homothermic mammals and birds the power of becoming themselves homothermic.

In birds the non-conducting coat is still supplied by the appendicular parts of feathers, while in mammals the homologous structure is not available, being invaginated into the follicle as the inner root-sheath. Under these circumstances a non-conducting coat has been supplied by a fresh formation of fine hairs. The transition was probably very gradual, and the latter are to be regarded as much later products than the large hairs. It is in harmony with these supposed changes that the small hairs of Ornithorhynchus depart in so many respects from the ancestral characters of the large hairs, and that they should be entirely wanting from those parts where the large hairs are, except as regards the medulla, the most scale-like, and possess the thickest inner root-sheath, and where the necessity for warmth is less imperative.

The invaginated inner root-sheath has, I believe, an important function in retaining the hair in its follicle. The hair itself, growing from the soft cells of the bulb, cannot be fixed very firmly, but the inner root-sheath pressed tightly between the hair and the outer sheath, and with its innermost cells imbri-

cated downwards and interlocking with the cuticular cells of the hair, which are imbricated upwards, gives to the hair a swollen base which prevents it from being drawn with ease through the narrow neck of the follicle. If it be forcibly torn out, the inner root-sheath accompanies it. When the hair is ultimately shed, its attachment has risen to a higher level in the wall of the outer root-sheath, so that it is no longer fixed in the manner described above.

The suggestions and hypotheses here put forward are not the result of a hasty consideration of the subject, but were deliberately adopted years ago as the best explanation of the new facts brought out by the investigation, and their relation to old facts which were imperfectly understood.

It may be fairly claimed for the views here expressed that they suggest a simple and probable morphological explanation of every structure in the hair or associated with it. The dermal papilla, epidermic bulb, medulla, hair-shaft, and inner root-sheath, all follow naturally from the invagination of a proto-Mammalian scale like that diagrammatically represented in woodcut fig. 2, while the outer root-sheath is clearly the walls of the pit into which the invagination took place. The further fact that fig. 2 is, except for the want of invagination, essentially similar to the hair of the young of the lowest mammal, lends additional support to the hypothesis here suggested.

If, however, the interpretations offered in this and other parts of the present paper be dismissed by the results of further investigation upon better material, the main facts upon which the interpretations rest will always remain, and, yielding as they do a considerable store of fresh knowledge about this most interesting of all mammals, must always have a value.

EXPLANATION OF PLATES 14, 15, & 15A,

Illustrating Professor E. B. Poulton's paper on "The Structure of the Bill and Hairs of Ornithorhynchus paradoxus, with a Discussion of the Homologies and Origin of Mammalian Hair."

PLATE 14.

The figures in this Plate illustrate the structure of the bill. The structure of the epidermis is indicated in Figs. 1 and 8. Figs. 1—7 deal with the tactile organs of the bill, Figs. 8—16 with the glands and their associated structures.

Figs. 4, 8, 9, 10, 11, and 12 were drawn from sections stained with carmine; while Figs. 3, 5, 6, 7, 13, 14, 15, and 16 were from sections stained with logwood. Fig. 1 was from a section stained with logwood and picric acid, Fig. 2 from one stained with carmine and picric acid. Cornified epidermic cells are indicated by a yellow colour.

Fig. 1.— × nearly 200 diameters. Vertical section through the surface of the bill (probably near the edge of the superior surface of the upper bill), showing a complete push-rod and parts of two others. The convex upper end of each rod, surrounded by a slight ridge, is clearly seen. Each rod is seen to consist, for the upper fourth of its length, of extremely thin curved epidermal plates, retaining traces of nuclei surrounded by pigment (compare Fig. 2). The corneous layer is not nearly so thick in the push-rod as in the general epidermis of the bill. Below the upper fourth of their length the rods are formed of imbricated cells with distinct nuclei, the layers being better shown in more highly magnified figures (Figs. 3 and 4). The same applies to the axial group of longitudinal filaments and the circle of similar structures shown in longitudinal section on each side of the group, and separated from it by a row of imbricated cells. The filaments are seen to diverge slightly at the lower end of the rod. Pigment is chiefly present at the sides of the rods, and especially among the lowest cell-layers forming the extreme base; but it also exists in the inner layers, as is shown in Fig. 4. The lower part of the rod is free from the general epidermis of the bill, being separated from it by a tubular dermal upgrowth, the upper part of which sends up papillary processes. Hence the dermis seen on each side of

the rods in Fig. 1 is partly a longitudinal section of the tube and partly that of the papillary processes (as seen in transverse section in Fig. 3). The lower end of the complete rod is seen to rest on three touch-bodies, of which two are in longitudinal and one in transverse section. Medullated nerve-fibres approach the touch-bodies, and a fibre is shown entering the base of one of them.

Fig. 2.—× rather over 400 diameters. Vertical section through the upper part of a push-rod and the adjacent corneous epidermis of the bill. From the same locality as Fig. 1. The thin flattened cell-plates form nearly hemispherical shells which, placed one over the other, build up this part of the structure. The form and arrangement suggest a structure which would easily yield to pressure, but would be instantly restored to the former level on its withdrawal.

Fig. 3.—× rather over 400 diameters. Horizontal section of the epidermis of the bill (locality unnoted, but appearance typical) taken rather below the corneal layer. The push-rod in transverse section is clearly seen to consist of the following layers, the epithelial cells being represented by their nuclei. (1) Centrally, the axial group of filaments: these are very highly refringent, and stain with great difficulty; they are probably partially or completely corneous. (2) A single layer of deeply staining epithelial cells. (3) The circle of filaments, similar to those of the axial group; they are arranged with great regularity. (4) A single layer of rather deeply staining epithelial cells. (5) A single layer of very faintly staining epithelial cells. (6) The outermost epithelial circle, seen by comparison with Fig. 4, to consist of several layers of cells which stain deeply. Outside this are the deeply staining fusiform cells of the general epidermis. Three papillary outgrowths are seen in section.

Fig. 4.—× over 600 diameters. Longitudinal section of a push-rod, with the transverse section diagrammatically rendered. From nearly the same locality as Fig. 1, but, in this case, from the very margin of the bill. The layers described in the last figure are here indicated by the corresponding numbers. The appearance represents the details as they can be made out with high powers and the most favorable sections. The filaments are seen to have a ladder-like appearance, apparently due to their constitution out of short sections, the length of which corresponds to the thickness of the cells of layer 2. The appearance suggests that each section may be contributed by the inner end of the adjacent cell. The same is true of the filaments of the circle (3) as regards the cells of layer 4, although in some cases the sections appeared rather to correspond with the outer ends of the cells of layer 2. The correspondence between the sections and adjacent cells is not well represented in the figure. The flattened imbricated cells of layers 2 and 4 are seen to be swollen at the spot where the nucleus is situated, where also there is a special accumulation of pigment. In transverse section of the rod, the cells of all the layers have the form of flattened curved plates, and

not the radial form indicated in the diagrammatic transverse section. They are, furthermore, far less numerous than in the latter, each plate curving round the rod for a considerable distance, as is indicated by the arrangement of the nuclei in Fig. 3.

Fig. 5.— × about 50 diameters. Horizontal section of one of the highly sensitive transverse ridges on the outer side of the upper surface of the lower bill (inside the mouth). The push-rods seen in transverse section are extremely numerous. Nearly all the layers shown in Figs. 3 and 4 can be made out, even with this low power. Fifteen gland-ducts are seen in transverse section, scattered between the twenty push-rods. In other parts these proportions are generally reversed. Many of the gland-ducts are surrounded by pigment. The right-hand upper push-rod has a distinct papillary upgrowth on each side of it. Higher powers show that two or more such papillæ are usually arranged round the other rods.

Fig. 6.— × about 50 diameters. A deeper horizontal section, nearer the middle of the length of the same ridge as that which supplied the material for Fig. 5. The section passes just below the lower ends of the push-rods, and shows the numerous groups of Pacinian bodies (from two to five in a group), each of which is placed under a rod (compare Fig. 1). Twenty-four groups are represented, together with nineteen gland-ducts, the proportion being about the same as in the last figure. When only a single Pacinian body is seen, it is probable that the rest of the group was not included in the section. Many of the gland-ducts are surrounded by pigment. Between the structures described is the dermis of the bill, which is concentrated to form a fibrous investment to both ducts and groups of nerve end-organs.

Fig. 7.— × rather over 400 diameters. A single group of Pacinian bodies from one of the ridges of the lower bill. The figure shows the essential similarity of these nerve end-organs to those previously described in the tongue of the same animal ('Quart. Journ. Micr. Sci.,' July, 1883).

Fig. 8.— × nearly 200 diameters. Vertical section through the surface of the upper bill, probably from the same locality as that described in Fig. 1, including a longitudinal section of a gland-duct on its way to the surface, together with the remarkable structures associated with it. The duct passes along the axis of an epithelial cylinder, which has many points of resemblance to a hair, shortened at both ends, so that it is flush with the general epidermic surface above, while its bulb is but little below the lowest layer of the epidermis. In favorable examples, however, as in that selected for figuring, the upper corneous end of the cylinder projects a little, and is surrounded by a distinct trench. Below the corneous stratum of the general epidermis the cylinder is surrounded by an epithelial layer (*o. r. s.*), which presents many points of resemblance to an outer root-sheath, from which the cylinder is seen to be in part free, a distinct space between the two being visible on both sides a little below the level A and on one side at the deeper level C. Below,

this layer is continuous with the outer and lower part of a large mass of epithelium bearing strong resemblance to a hair-bulb, but separated from the rest of the mass by a space (*sp.*) containing small branched cells. For the proper understanding of this part of the structure better material is much to be desired, for it is probable that considerable post-mortem changes had occurred. Within the supposed outer root-sheath the cylinder (the supposed hair) is surrounded by flattened cells (*c.*), which suggest the cuticle or possibly the inner root-sheath or both of these. This layer also arises from the supposed bulb. The central part of the cylinder consists below of polyhedral cells like those of the bulb, passing above into corneous fusiform scales with a longitudinal arrangement. The gland-duct (*d.*) passes into the lower end of the bulb, remaining distinct from the epithelium of the latter. In this lower part of the bulb the cells stain more deeply than those of the bulb, and their outlines are less distinct (compare Fig. 11). The duct is at first straight, but subsequently pursues a twisted course in the bulb, generally to a more marked extent than in the example figured. In the upper part of the bulb the duct becomes surrounded by a single layer of cubical cells, still staining rather more deeply than those external to them, but with distinct outlines. Above the point where the cylinder becomes corneous the duct appears to traverse its axis without any proper investment, the walls being extremely irregular and the lumen of a radiate star-like form in transverse section (compare Figs. 9 and 10). The whole arrangement suggests that the duct may have penetrated the bulb of a shortened and rudimentary hair by way of the papilla, and found its way along the medulla. Immediately below the bulb the duct is surrounded by a ganglion (*gn.*) containing large nerve-cells and medullated nerve-fibres, in which nodes of Ranvier are commonly noticed. Below this a large medullated nerve (*n.*) and the gland-duct (*d'.*) are seen in transverse section, while a curved gland-tube (*gld.*) is shown to the left. The structure is evidently that of a Mammalian sweat-gland, a single layer of cubical gland-cells being surrounded by delicate fusiform smooth muscle-cells longitudinally arranged.

The following four sections represent horizontal transverse sections at successively deeper levels of a gland-duct like that shown in Fig. 8, together with the associated structures. All probably come from a very similar locality on the upper bill. All are magnified rather over 400 diameters.

Fig. 9.—Transverse section of the duct at about the level marked A in Fig. 8. Six papillary upgrowths mark the line of separation between the epithelium round the duct and the general epidermis of the bill. The cornification is more extensive than in Fig. 8.

Fig. 10.—Transverse section of the duct at about the level marked B in Fig. 8. The lumen appears stellate in this and the previous figure. Of the six papillæ seen at a higher level, three have coalesced, while three remain distinct. Just below this level all six pass into the continuous dermal sheath

which surrounds the lower part of the epithelial cylinder traversed by the duct. The cells immediately round the duct tend to split away from those placed more peripherally, suggesting the separation of a hair from its outer root-sheath.

FIG. 11.—Transverse section of the duct at about the level marked C in Fig. 8. This is the region of the bulb of the supposed hair. The difference between the epithelium of the duct (*d.*) and that of the supposed bulb is clearly shown, although the duct resembles that which is seen at a rather lower level than C in Fig. 8. The deeper staining of the duct (*d.*), and especially of its innermost layer, is very characteristic in these sections. The supposed cuticle (*c.*) and outer root-sheath (*o. r. s.*) are clearly seen.

FIG. 12.—Transverse section of the duct at about the level marked D in Fig. 8. The duct is surrounded by the ganglion containing many ganglion cells. One of these is seen to give off a long process; a medullated nerve-fibre with a node of Ranvier is also present. Both the duct and the ganglion are surrounded by a fibrous sheath.

The following three figures represent various forms of the duct; all are magnified about 50 diameters.

FIG. 13.—The coiling of the duct in the lower end of the epithelial cylinder (the supposed hair) is well seen. The resemblance of the upper end of the cylinder to a truncated hair is especially distinct in this and Fig. 15. An S-like curve of cylinder and duct in the upper layers of the epidermis is shown in this and Fig. 15. It is a very common appearance.

FIG. 14.—A very common form at the posterior part of the upper surface of the upper bill.

FIG. 15.—A form in which the epithelial cylinder is very slightly developed. It occurs intermixed with those of the commoner type (Figs. 8 and 13).

FIG. 16.—× nearly 200 diameters. This figure shows the form of two ducts, &c., in the bill of a young Ornithorhynchus, 8·3 centimetres long in the curled-up attitude. The "bulbs" at the lower end of the cylinders are not only extremely well developed, but are more deeply placed than in the mature animal. Just below the level of the bulbs, large medullated nerves (diagrammatically rendered in the figure) extend in a horizonta layer, uniting to form ganglia round the bases of the bulbs themselves. It is very unfortunate that histological details could not be made out.

PLATE 15.

The figures in this plate illustrate the structure of the hairs and the structures associated with them. Figs. 17, 18, and 25 represent structures in the mature animal; the remaining figures represent those of the young animal 8·3 centimetres long, in which the large hairs alone had appeared above the surface of the skin.

FIG. 17.—× nearly 200 diameters. Transverse section of a group of hairs from the middle of the back. The section is taken just below the epidermis. Groups like this apparently make up the fur which clothes the body of the animal, although modifications occur on the tail and limbs. The constituents of the group pierce the subepithelial tissue obliquely, and overlap each other on emergence. Those in the lower part of the figure are overlapped by those in its upper part, which are situated anteriorly to them. Most anteriorly of all is usually found the duct (*d.*) of a gland resembling the Mammalian sweat-gland. It and the more deeply-placed gland-tube are found along the anterior margin of the outer root-sheath (*o. r. s.*) of the large hair, or between it and one of the two anterior bundles of small hairs (Fig. 18, *g.*). Behind the duct is the most important member of the group—the large hair contained in its outer root-sheath (*o. r. s.*). These hairs succeed each other very rapidly and always in an antero-posterior direction, so that the great majority of sections show two of them associated with one outer root-sheath. The shield-like end of the developing large hair (*l. h.*) is seen anteriorly in the lumen of the follicle, while behind it is the attenuated unpigmented basal part of a fully formed hair (*l'. h'.*) Behind, on either side, are two bundles of small hairs, each bundle being enclosed in a single epithelial ring. The majority of sections in each bundle are those of the attenuated pigmentless bases of fully formed hairs, while the minority are those of various parts of the shaft of hairs which are still growing from a bulb, and in these pigment is seen to be present.

FIG. 18.—× nearly 200 diameters. A transverse section through a similar group from the same locality taken at a somewhat lower level. The duct has now passed into a gland-tube (*g.*) in which peripheral longitudinal smooth muscle-cells and central gland-cells are seen. The expanded end of the young large hair (*l. h.*) is here cut nearer to the bulb, and is only pigmented in its lower part. The medulla is distinct as a group of cells which still remain protoplasmic and stain deeply. After emerging at the surface these soft cells dry up, and give rise to the ordinary hair medulla with its enclosed air-bubbles. The cuticle to which the reference letters (*l. h.*) point is seen to be far thicker on the exposed anterior surface than elsewhere. Comparison with Fig. 17 shows that nearer the tip of the hair it possesses a uniform thickness. The base of the mature large hair (*l'. h'.*) is, at this deeper level, enclosed in the posterior wall of the outer root-sheath, and is irregular in outline. A little below this point it terminates in an irregular rounded extremity, sometimes

sending out processes which pass between the adjacent epithelial cells. The younger hair, on the other hand, passes down to a great depth and ends in a bulb. The small hairs in the four bundles are seen to have separated, each being enclosed in an epithelial tube corresponding to an outer root-sheath, but the walls of the tubes are at this level continuous peripherally in each bundle. Below, the pigmented younger hairs are continued to a far deeper level, their outer root-sheaths expanding into bulbs, while the unpigmented bases of fully-formed hairs terminate without bulbs very slightly below this horizon. Indeed two of them (one in each of the right-hand bundles) are already terminating, and have ceased to be corneous.

Fig. 19.—× rather over 400 diameters. Transverse section of one large and many smaller hairs from the middle of the back of the young Ornithorhynchus. The sections are of the first-formed hairs, and as these are by no means fully formed, only the tips of the large ones having appeared above the skin, no traces of the successional hairs are to be seen. The upper part of the large hair in the figure represents its anterior and upper side on emergence, and it is seen that the cuticle (*c.*) is here thicker, while the pigment is contained in the hair-cells which are undermost in the natural position. The medulla is represented in section by four protoplasmic cells, and the nuclei of the hair-cells between this and the thickest cuticle stained with logwood. Outside the cuticle is a layer (*i. r. s.*), which is very characteristic of Ornithorhynchus, surrounding the hair above the neck of the bulb for a considerable part of its passage through the dermal tissues. It consists of anastomosing, apparently corneous fibres, representing the inner root-sheath to which the homogeneous deeply staining layer outside it probably also belongs. The outer root-sheath (*o. r. s.*) is at this horizon extremely delicate and thin, and is succeeded by a lymph space. The entire sections of four small hairs are seen, as well as parts of four others. Four small hairs are at this age usually found beneath a large one, and each of them appears to represent one of the four groups of small hairs found beneath each large one in the mature animal. The four entire sections probably represent those which attend the large hair in the section. The two inner ones are cut through at the level of their bulbs, and centrally the papillæ are seen in section. The two outer indicate the structure at a higher level as seen in section, the shaft being composed of six radially arranged pigmented hair-cells surrounded by a cuticle followed by a thick inner and irregular outer root-sheath and lymph space. It must be borne in mind that the delicate tissues of the young Ornithorhynchus had not been prepared for histological investigation, and that it was therefore extremely difficult to form an opinion upon some of the layers. This caution applies especially to the layers interpreted as outer root-sheath and the outer part of inner root-sheath in Figs. 19 and 20 and the former in Fig. 23.

Fig. 20.—× rather over 400 diameters. A section of one of the large hairs from the same part of the same animal as Fig. 19, taken at a rather deeper level.

The reference letters correspond to those of Fig. 19. In the centre of the hair-cells is a cavity in which the papilla was doubtless contained, for in Ornithorhynchus the papillæ extend above the bulb into the neck (compare Fig. 23). The inner root-sheath (*i. r. s.*) is apparently divided into two layers; which, however, are less sharply marked off from each other than in Fig. 23. The cellular nature of the inner part is apparent. The upper surface of the hair is rendered very distinct by its immensely thickened cuticle and by the absence of pigment.

Fig. 21.—× rather over 400 diameters. Transverse section of large hair in tail of young Ornithorhynchus. The pigmented hair-cells constitute the thickness of the shaft, and no medulla is visible. A superficial pigmentless layer is probably the cuticle. The inner root-sheath (*i. r. s.*) is exceedingly thick and made up of fibres which are polyhedral and irregular in section, and its innermost part appears to be condensed into a continuous layer immediately surrounding the shaft of the hair. The outer root-sheath (*o. r. s.*) is very distinct. A lymph space separates the last layer from the hair-sac.

Fig. 22.—× rather over 400 diameters. A transverse section of a rather small hair from the tail of the same animal, taken at a somewhat deeper level immediately above the bulb. The inner root-sheath is here divided into two well-marked layers, the inner of which is not corneous and stains very deeply in logwood. At a still deeper level this would be true of the whole sheath. In other respects the sections are essentially similar.

Fig. 23.—× nearly 200 diameters. A longitudinal vertical section through the bulb and neck of a large hair from the middle of the back of the same animal. The immense size and upward extension of the papilla is the most remarkable feature in the section. The tip, to which the reference letter *p.* points, is well above the bulb of the hair, and has reached a horizon at which the hair-cells have become distinctly fusiform. The papilla itself contains capillaries and branched cells. The upper surface of the hair is on the left side, and is at once distinguished by its thick cuticle (*c.*) and pigmentless cells. The root-sheaths are thin, and their structure indistinct. The section being exactly along the middle line of the hair there was nothing to keep the two halves together, consequently they have fallen outwards so that the structure appears to be wider above the papilla. If this had not happened it would have been much narrower than the bulb, and the chink in which the letter *p.* is placed would have been obliterated, although in estimating the diameter we must allow for the medullary cells which have been accidentally removed in the manipulation.

Fig. 24.—× nearly 200 diameters. A longitudinal section of a large hair on the head of the same animal. The section was somewhat oblique, passing through the middle line of the hair at the point where the latter is represented in diagrammatic transverse section. At this point and just below it the deeply staining medullary cells are seen surrounded by the pigmented hair-cells, and these by the cuticle (*c.*). The inner root-sheath (*i. r. s.*) is seen

from within as well as in longitudinal section, and is clearly shown to consist of a network of corneous fibres enclosing longitudinal fusiform spaces through which the outer root-sheath (*o. r. s.*) is seen. At the upper end the section becomes more tangential, and hence the more obliquely cut edge of the outer root-sheath gives an erroneous impression of greater thickness at this point.

Fig. 25.—× nearly 200 diameters. A gland tube and duct opening into the bay between the flange-like posterior extension of the upper bill and the hairy surface of the head. The secretory part of the gland is seen to possess the structure typical of the Mammalian sweat-gland. The duct is, however, unusually wide. In this position the glands were peculiar in opening on the surface independently of hairs or hair-like epidermic processes.

PLATE 15a.

The young Ornithorhynchus paradoxus of which the hairs are described in this paper, and are represented in Plate 15, figs. 19—24. The animal is represented of the natural size, as seen from the left side in Fig. 1, from the ventral aspect in Fig. 2. The skin appeared to be quite smooth and bare, but closer examination showed that the tips of the large hairs had emerged from the surface, the small ones being still concealed beneath it.

A Contribution to our Knowledge of the Oligochæta of Tropical Eastern Africa.

By

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With Plates 16 and 17.

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1. Introductory.

THERE seems to be no doubt that at present tropical Africa furnishes the most remarkable and interesting representatives of the terrestrial Oligochæta. The family Eudrilidæ have their headquarters there; indeed, with the exception of the almost cosmopolitan genus Eudrilus, the family is confined to the Ethiopian region, not even extending, so far as we know at present, into the more northern part of the continent.

Eudrilidæ are already known from both the west and from the east side of Africa; they appear to abound principally in the equatorial region, though by no means unknown from

more southerly districts. The forms from the east have been mainly described by Dr. Michaelsen[1]; those from the western side of the continent by myself.[2] It has been shown by these investigations that, as a rule, the east and west of tropical Africa are inhabited by different genera, and always by different species. It also appears that, on the whole, the number of worms belonging to this family is greater on the east coast than on the west.

The peculiar interest attaching to this group of Oligochæta, independently of their distribution, concerns the structure of the reproductive organs; in most of the members of the group there are no spermatothecæ homologous with those of other Oligochæta; the place of these organs is taken by cœlomic sacs which acquire an opening to the exterior; rarely are there true spermatothecæ in addition to these cœlomic sacs; when such spermatothecæ are present they are partially or entirely enclosed by the sacs in question. In the more specialised members of the family the ovaries are also enclosed in sacs which communicate with the egg sacs and sometimes also with the spermatothecal sac. The Eudrilidæ, in fact, are an altogether remarkable family of Oligochæta, and it is desirable that our knowledge of them should be perfected. I am therefore glad to be able to contribute towards that end by the following account of a number of new forms collected in Zanzibar and Mombasa. I was enabled to acquire this material through the liberality of the Government Grant Committee of the Royal Society, who awarded me £100, with which I paid the costs of a collector; I was so fortunate as to secure the assistance of Mr. Frank Finn, to whom I am indebted for the careful way in which he carried out my instructions in the matter of preservation, &c.

[1] "Beschreibung der von Herrn Dr. F. Stuhlmann im Müirdungs gebiet des Sambesi gesammelten Terricolen," 'J. B. Hamb. wiss. Anat.,' vii. "Beschreibung der von Herrn Dr. F. Stuhlmann auf Sansibar und dem gegenüberliegenden Festlande gesammelten Terricolen," ibid., ix.

[2] "On the Structure of Two New Genera of Earthworms, &c.," 'Quart. Journ. Micr. Sci.,' vol. xxxii. "On the Structure of an Earthworm allied to Nemertodrilus, &c.," ibid.

I received from him a very large number of Oligochæta belonging to thirteen species at least; of these I describe eight in the present paper as new. The eight new species are the following:

Eudriloides Cotterilli, n. sp.
Eudriloides brunneus, n. sp.
Polytoreutus violaceus, n. sp.
Polytoreutus Finni, n. sp.
Polytoreutus kilindinensis, n. sp.
Pareudrilus stagnalis, n. gen., n. sp.
Gordiodrilus zanzibaricus, n. sp.
Alluroides Pordagei, n. sp.

In addition to these there were numerous examples in the collection of species apparently identical with Michaelsen's Stuhlmannia variabilis. This species is indeed to all appearance the most abundant form of Eudrilid in the regions visited by Mr. Finn. Besides the specimens preserved by Mr. Finn, he brought me a large number of living Oligochæta; the bulk of these were of this species.

Another species abundant in the gatherings was a Benhamia of small size, which I have not minutely studied as it showed no noteworthy differences from the smaller species described by Michaelsen.

In the mud from swamps brought home there was an abundant supply of a Dero with two long processes in addition to the four "gills;" this species seems to be identical with that named Dero Mülleri by Bousfield; in the same mud I found a Nais and an Enchytræid, neither of which have I identified; these two species, however, were immature, and they did not exhibit any characters of particular interest.

The worms were all of them, with the exception of the species of Eudriloides, the Benhamia, and the Polytoreutus, found in, or at the margin of swamps. The aquatic character of these Eudrilids is perhaps to be noted in connection with the total absence of dorsal pores, a character already known to distinguish the Eudrilidæ from the majority of "earthworms." The other forms were collected in soil outside a bungalow,

which was kept continually moist with the "slops" of the household. In no other situations were any Oligochæta to be found even after or during rain. It seems probable that in the dry season they retire deep within the ground or take refuge in swampy ground. As to the former suggestion, it is only supported by the presence of the worms in moist ground, for Mr. Finn informs me that he examined a deep trench in the course of its digging, and did not come upon any traces of these animals at all. It is possible that the comparative rarity of terrestrial Oligochæta in other tropical countries is to be accounted for by the fact that they lurk in swamps, and only come forth when the ground is thoroughly soaked, and fit for them to traverse. On the west coast of Africa the earthworms seem to be more purely terrestrial in habit. I hear from Mr. Finn that I am indirectly indebted to the kindness of General Mathews, principal minister of His Highness the Sultan of Zanzibar, to Mr. Pordage, to Mr. Macalister, and to Mr. Cotterill, for some of the material. To these gentlemen I beg to tender my thanks.

2. Description of New Species.

Eudriloides Cotterilli, n. sp. (figs. 1, 15, 16, 18—20).

A considerable number of examples of this species were collected by Mr. Cotterill outside a house at Kilindini. I have studied the species partly by the section method, and partly by dissection, and subsequent examination in glycerine.

The species is a small one—an inch or so when preserved.

The specimens were preserved with Perenyi's fluid and had, after preservation, hardly any definable colour, but the paired nephridia were very conspicuous as white masses shining through the transparent skin.

The prostomium of the worm is not large, nor does it appear to be continued by grooves on to the buccal segment. In longitudinal sections the prostomium seemed to be divided by a transverse fissure, a character which is known to distinguish Phreoryctes but has not been met with elsewhere in

this group. The setæ begin on the 2nd segment; they are strictly paired, and rather small in size, of the usual form, without any ornamentation. The two ventral pairs are rather further apart from each other than is either of them from the lateral pair of its side, but all the setæ are distinctly upon the ventral surface of the body. They appear to be absent from a few segments of the body. I did not find the ventral pair on the 13th segment on either side of the body, nor were there any traces to be discovered on any of the clitellar segments of either ventral or lateral pairs. They re-commence just on a level with the posterior boundary of the male papilla.

The clitellum is saddle-shaped. It occupies the Segments XIV—XVII. The median ventral area which is not part of the clitellum is chiefly occupied by the prominent pores of the reproductive organs. The whole area is hour-glass-shaped, being narrower in the middle than at either of the two ends. Independently of the very prominent papillæ which bear the reproductive orifices, there is a single papilla upon the 11th segment of an oval form. It lies on the posterior half of the segment, just causing a slight convexity of the boundary line between this segment and the 12th. The papilla lies entirely between the ventral setæ. It ends on each side just on a level with the inner of the two setæ of that pair. The transverse diameter of the papilla is greater than its antero-posterior diameter. The median spermatothecal pore lies on the line between Segments XIII/XIV. The actual orifice itself is circular and not large, not so large as the male pore. It is borne upon a very prominent swelling of the body-wall, which may extend as far forwards as the posterior boundary of Segment XII. In some specimens the terminal section of the spermatothecal sac is protruded from the aperture.

The oviducal pores are not conspicuous until the worm is carefully examined with a tolerably high power of the microscope; they are invisible under a low power; each aperture is on the 14th segment; it lies in a position exactly corresponding to the lateral setæ.

The single median male pore is a transversely elongated

aperture on the boundary line between Segments XVII/XVIII; it is curved, the concavity being forwards; the two ends of the orifice are wider than the middle part—like the mouth of an Actinozoon; out of this orifice protrude the penial setæ; the aperture is upon a conspicuous papilla, which is larger than that which bears the spermatothecal pore; there are two small supplementary papillæ at the posterior angles of the cushion.

The external characters distinguish this species from the three others, viz. Eudriloides parvus, E. gypsatus, and E. titanotus.

In the first of these species there is a median papilla upon the 19th segment, but none is mentioned by Michaelsen upon the 11th. No papillæ are mentioned in the remaining two species; Eudriloides Cotterilli has not, as have the other species, a complete clitellum.

Vascular System.—There is at present no information as to the vascular system of this genus. Michaelsen's two papers,[1] which deal with the only species of Eudriloides known previously to the publication of this memoir, contain not a syllable about the blood-vessels. My own notes upon the subject, though few, will therefore be of some use. The dorsal vessel has a thick coating of peritoneal cells, and its walls are of some thickness; in this it contrasts with the supra-intestinal vessel, which, although of greater calibre, has thin walls; the ventral vessel has also a covering of quite conspicuous cells. In the 10th and 11th segments there are a pair of perivisceral vessels which arise from the supra-intestinal vessel alone. I have ascertained that they have no connection at all with the dorsal vessel. These "hearts" have thick muscular walls, which commence abruptly at their origin from the supra-intestinal trunk; they are furnished along their course with frequent valves, and the opening into the ventral vessel is guarded with valves, as is also that into the supra-intestinal; in front of these are a series of perivisceral trunks of less calibre which arise from the dorsal vessel only, and have no connection with the supra-intestinal. The dorsal

[1] Loc. cit. (on p. 201).

vessel has valves at the points where it perforates each septum.

The alimentary canal has a gizzard in Segment VI; the œsophagus has a number of pairs of peculiar glands, which are separately described in connection with those of other Eudrilids below. The intestine begins in Segment XV. The œsophagus is very vascular.

The first septum separates Segments IV/V; it is very delicate; behind this are five very thick septa, and then follow two others which are somewhat thicker than those which follow them.

The nephridia commence in Segment IV. They appear to open in front of the ventral setæ; in any case their duct was traced into the body-wall on a level with the ventral setæ; but whether it expands into a plexus like that of Libyodrilus, or opens at once on to the exterior, I am unable to say; the nephridial duct is not a conspicuous sac, as in some other Eudrilidæ, but a tube having an intra-cellular duct.

Reproductive organs.—This species has, as have the other species of the genus, only a single pair of testes; as is customary when there is but a single pair of these gonads, they lie in the 11th segment. Each testis is attached to the front wall of Segment XI; its shape is a little unusual. The testis is a curved rod of narrow dimensions, only a little broader than elsewhere near to its origin from the septum; if it were to lie in a perfectly straight line in its segment, as the testes usually do, it would reach as far as the funnels of the sperm ducts; it therefore has to be coiled in order to get it out of the way. The cells of which the testis are composed are not very distinct; the nuclei, however, are; these nuclei are larger and clearer at the base of the gonad.

The sperm-sacs lie in Segment XII; they depend from the anterior septum of this segment; they are fused together at their origin, and the question therefore arises as to whether we are to consider that there are two sacs or only a single bifid sac. The latter view would bring the sperm-sacs into correspondence with other parts of the generative apparatus; in any case they are not to be distinguished at their actual

origin. The sperm-sacs have a slightly racemose appearance; they are attached to the septum by a stalk; this stalk is hollow, and seems to open into the cavity of the 11th segment; it is of course lined by peritoneum, which is especially thick on that part of septum near to the origin of the sacs. The walls of the sacs are muscular and thin; there are also trabeculæ of muscular fibres which divide the interior of the sacs into compartments; these spaces are full of developing sperm. Michaelsen has described in Eudriloides gypsatus, in addition to these sacs, a sac in the 11th segment. I have looked carefully for this, but can only find a mass of sperm in that segment. This mass of sperm is not enclosed by any walls, and there are no blood-vessels for the supply of any sac, such as are abundantly obvious in the case of the sperm-sacs of the 12th segment.

The sperm duct runs along the body-wall just at the line of implantation of the ventral setæ; it is accompanied in its course by a blood-vessel. Near to the external orifice of the atria the sperm-duct perforates the outer coat of the atrium of its own side, and comes to lie where it is represented in fig. 1. Anteriorly the sperm-duct of each side opens into the cavity of the 11th segment by a large and much folded funnel; the two funnels together occupy a great deal of the space in the 11th segment; above the nerve cord the two funnels become fused together. The atria extend through three or four segments; they lie side by side, and are never coiled; this coiling, which is often seen in the long atria of other species, is rendered impossible in the present case by the thick muscular coat which forms the outer layer of the atria. This muscular layer consists of longitudinal and circular fibres; the circular fibres are internal. The epithelium lining the atrium appears to consist of two layers, but these are not by any means so thick as in other Eudrilidæ; in transverse sections of the atrium the lumen is seen to be crescentic; the convexity of the crescent is dorsal; below this lies the sperm-duct, which, as already stated, lies within the atrium: the sperm-duct passes just between the epithelium and the muscular layers; it is accompanied by a blood-vessel. Towards the external pore of the

two atria the lumen of each gets to be more and more oval in outline. As in other species of the genus Eudriloides, the aperture of the atria is furnished with penial setæ; there are two of these, one on each side; the penial seta is curved into an S-shape; the curvature is much more pronounced than that of the ordinary setæ; the free tip of the seta appears to be bifid; it is ornamented with a series of minute denticulations; these occupy a restricted area just in front of the actual tip of the seta; their shape can be understood by an inspection of the accompanying figure (fig. 20).

There is in connection with the male efferent apparatus a very complicated arrangement of muscles, recalling in many particulars the corresponding structures in Eudriloides brunneus. These structures are best elucidated in glycerine preparations of the worm from which the alimentary tract has been removed. In such a preparation the two penial setæ will be seen on either side of the male pore lying somewhat obliquely; near to the distal end of each seta a strong bundle of muscles is attached; the actual attachment is not extensive, but the muscles rapidly fan out, and where they are inserted on to the body-wall form a bundle of considerable dimensions. The muscular fibres forming these two bundles are bound up into separate muscles, as is shown in the figure illustrating this copulatory apparatus (fig. 18). On the opposite side of each seta there is another strip of muscles which runs obliquely almost in the same straight line as the first mentioned set; this bundle of muscles is, however, of equal diameter throughout, and is not nearly so wide as the first. It seems clear that these two sets of muscles have an opposite effect, moving the penial seta in different directions. We now come to the muscles of the bursa copulatrix. The two atria join to form a tube, which is much narrower than either of themselves; this unpaired tube is covered by a layer of muscles which runs transversely across the body, being attached to the body-wall in the immediate neighbourhood of the penial seta on each side. From the same point of origin arise a few fibres which are inserted upon the tube itself, and a still more slender

bundle which is inserted upon each of the two atria just in front of the point where they become fused. On the opposite side of the male pore is a bundle of muscular fibres running longitudinally. The total effect of the contraction of all these muscles, as it appears to me, would be the protrusion of the terminal apparatus of the male organs. I think that any of these muscles could play the part of retractors when the terminal sac is protruded; they could, I should imagine, serve both as retractors and protractors, according to the position of the organ.

The ovaries are in the 13th segment; they are unenclosed by any sac; the oviducts opposite to them open partly into the cavity of the 13th segment and partly into the egg-sac. In the independence of the ovaries, egg-sacs, and spermatothecal sac, the present species agrees with other Eudriloides.

The spermatothecal sac is much like that of Eudriloides brunneus; it opens on to the 13th segment and extends a little way in front of its external pore and reaches for some way behind it—as far as the 17th segment. I have studied the minute structure in a nearly mature specimen (quite mature except as regards the clitellum), and in a much younger specimen. The part of the spermatothecal sac lying in front of the aperture is not in any way different in structure from the rest. The walls of the sac are much thinner posteriorly than anteriorly; they are lined by a layer of large cells which are covered externally by a muscular coat; at the pore the structure is a little difficult to understand; it is shown in fig. 16. I could find no actual orifice, perhaps to be accounted for by the worm not being fully mature. The epidermis is thin just below the pouch and the muscular layers of the body-wall have disappeared. The spermatotheca is lined by the thick layer of cells referred to. These get so close together where the lumen narrows towards the pore that the lumen is entirely obliterated. It may be that this arrangement of the cells means that the protrusible termination of the male efferent apparatus can be thrust into the spermatotheca, but that the sperm cannot escape from the sac. The ventral half

of the pouch is encircled by a cup-shaped layer of epithelium whose cells are of an altogether different character. These cells are regular columnar cells with the nucleus at about the middle. They have every appearance of being epidermic cells invaginated, but I could not find that they were at any point continuous with the epidermis; there was a slight break on either side. This, however, is not fatal to the view that they are invaginated epidermic cells. These cells, so easily distinguishable by their characters from the thick mass of cells occupying the inner surface of the spermatothecal sac, do not immediately abut upon the latter; the two layers are separated by a thick, non-staining membrane which has every appearance of being of a chitinous nature; it is homogeneous and of a faint horn colour; it completely divides the two layers of cells spoken of. This species has, like Eudriloides brunneus, glands at the sides of the spermatothecal sac (see fig. 19). These have, apparently, precisely the same structure as in that species, and need not therefore be particularly described; there is, however, but a single pair of them. The ducts of these glands open partly on the exterior direct, and partly through the layer of cells already spoken of and presumed to be formed by an invagination of the epidermis. This is additional evidence of the justice of this interpretation of the cells in question.

In a younger specimen of the species the spermatothecal sac was less fully developed; the posterior part of the sac is very thin-walled, and lies to one side of the nerve-cord; it looks like a piece of a septum detached, and has a roughly circular contour. Following the course of the sac in a series of sections, it is seen to get beneath the nerve-cord and to lose its lumen; at the same time it decreases in diameter; at the external aperture there is a protuberance of the body-wall in which there is a slit-like crescentic lumen bordered by tall columnar cells; a lumen also suddenly appears in the dorsal part of the sac which is quite independent of the crescentic lumen referred to; this, indeed, is merely the border line between the tall columnar cells, which I believe to be an invagination of the epidermis,

and the cells lining the spermatothecal sac. This specimen was remarkable for a plug of cells filling the lumen of the sac just where it narrows towards the pore. The plug of cells projects a little way into the lumen, as shown in the figure (fig. 16), and is furthermore rendered obvious by its less staining and by a fibrous appearance with scattered nuclei. In the more mature worm I could distinguish no such plug. Underneath the epidermis the mass of cells forming this plug spreads out into a more extensive layer.

One of the three individuals which I examined by longitudinal sections showed a difference from the typical structure of the genus in the presence of two pairs of sperm-duct funnels. To these corresponded two pairs of testes. The additional pair was in Segment x. This segment, like the following, was filled with a mass of developing sperm not contained in a sperm-sac or sperm reservoir. In other particulars I could detect no differences from other specimens. It should be stated, however, that the penial setæ could not be studied. These setæ are, of course, frequently most useful in distinguishing species. It must, therefore, be left undecided as to whether this worm is a distinct species of Eudriloides or is only a variety of Eudriloides Cotterilli.

Eudriloides brunneus, n. sp. (figs. 2, 10, 21—23).

Of this new species of Eudriloides I have examined four examples; two were dissected and two examined by means of transverse sections.

As compared with the first species of Eudriloides described in the present communication, this is large; it is not, however, quite so large as Michaelsen's Eudriloides gypsatus.

The colour of the species was of a uniform greyish brown (after preservation in alcohol); the setæ are exceedingly minute, so as to be quite invisible when the worm is examined by a hand lens alone. Michaelsen has commented upon the minute setæ of Eudriloides gypsatus.

The clitellum was not very distinct; it appears to occupy the greater part of Segments xiv—xvii; the clitellum is not

developed upon the ventral surface of the body; the segments of which it is composed are a little difficult to map on account of the fact that the segments are subdivided by numerous transverse furrows, which do not correspond to the actual segments themselves. The arrangement is shown in the accompanying figure (fig. 10). Behind the median spermatothecal pore, which lies upon the 13th segment, there is a furrow which is the boundary line of Segments XIII/XIV. This latter segment bears a median genital papilla of an oval form, the long axis of the papilla being disposed transversely; in front of and behind this papilla is a short furrow; then follow five other transverse furrows, the last of which marks the line between Segments XVI/XVII; the clitellum is developed laterally in the region which is occupied by the various furrows which have been described; on the 16th segment is a pair of genital papillæ, one on either side of the median line; behind the male pore is a single and median papilla upon the boundary line of Segments XIX/XX.

The spermatothecal pore is upon the 13th segment; it is very conspicuous, being borne upon a prominent projection, which is no doubt retractile. The male pore is even more conspicuous, and is of about the same area.

The nephridia of this species appear on a dissection to be paired structures like those of other Eudrilidæ. This is, indeed, the case, but the duct leading to the exterior forms a network within the integument, as in the genus Libyodrilus, where I have lately described it.[1] I have mainly studied the nephridial system of this worm in the anterior segments of the body; in transverse sections through one of the anterior segments—the ninth, I think—two longitudinal ducts are observable running just to the inside of the longitudinal muscular layer in the peritoneum on each side of the body. These ducts correspond in position with the pairs of setæ; the inner of the two on each side is the larger. Near to the septum dividing the segment from the one in front the inner duct

[1] "On the Structure of an Earthworm allied to Nemertodrilus, &c.," 'Quart. Journ. Micr. Sci.,' vol. xxxii, p. 553.

became continuous with the nephridium, and at that point gave off a duct which penetrated the body-wall and apparently opened on to the exterior, though I did not succeed in discovering the actual pore. Following the duct back, the longitudinal duct was found to vary in calibre from place to place; it was sometimes so reduced as to be very nearly invisible; at other times it became of much greater calibre than the average. In these places it seemed as if the duct formed a kind of rete. In the one segment I counted three or four of these retia; in the same segment three or four branches arose from the longitudinal duct to apparently reach the exterior. At the point where the septum was attached to the body-wall the nephridial duct penetrated still deeper within the longitudinal muscular coat. When the septum lifted away from the body-wall, the inner of the two longitudinal ducts was found to have resumed its original position. Immediately after the septum a branch was given off from the vessel which, penetrating into the body-wall, passed round the circumference of the body, ultimately joining the outer of the two longitudinal ducts. I confess that the actual junction was not observed, but the tube was traced up to a very minute distance away from the second of the two longitudinal vessels; in front of this there is a connection by way of the peritoneum—a duct, that is to say, runs from one longitudinal duct to the other in the peritoneum. Here, again, I was not able to find the actual opening at both ends; but I have no doubt, from the appearances presented, that this takes place. The second longitudinal duct—that running on a level with the outer pair of setæ—is not dilated, and shows no such retia as the inner duct; nor does it appear to give off any branches penetrating the integument and reaching the exterior; in other segments, and more particularly in the region of the body occupied by the clitellum, I could not find the connection of the nephridia from segment to segment, such as undoubtedly occurs in some, at any rate, of the anterior segments. The nephridial system of this species, therefore, is constructed on the plan of that which characterises the genus Libyodrilus, but is in a less differ-

entiated condition. The integumental plexus appears to be much less developed in Eudriloides than in Libyodrilus. After finding that this species of Eudriloides showed the above mentioned resemblances to Libyodrilus, I examined other species, with a view to discovering how far they agreed with the present. In Pareudrilus something of the same kind seems to occur (see below). In Stuhlmannia variabilis I traced the nephridial duct into the body-wall at the inner pair of setæ; instead of opening on to the exterior opposite to the point where it entered the body-wall, the tube passed along the body-wall below the circular muscular layer, and eventually opened on to the exterior on a level with the outer pair of setæ. In one instance, at any rate, I feel sure that the tube did not extend further than this point, but whether there was more than one opening on to the exterior for each nephridium I am not able to say with certainty. I think that in Eudriloides Cotterilli the same state of affairs is found. In the two latter cases the small size of the worms was a matter of difficulty; the corresponding fineness of the tubes rendered their discovery a matter of greater difficulty than in Eudriloides brunneus. I am almost inclined to think that all those species of Eudrilids in which Michaelsen has described ventral nephridiopores will be found to have a nephridial system like that of the species described here. One is tempted, in the instances brought forward here, to associate the complexity of the integumental plexus with the size of the worm. In Libyodrilus and in Eudriloides brunneus, which are the two largest species in which the nephridial system has been investigated, it is apparently the most complex; in Stuhlmannia, at any rate, it seems to be less complex. The only time that I was able to follow out the tube from the point where it entered the body-wall to its external pore, it seemed to me to pass straight from opposite the inner pair of setæ to the aperture on a level with the outer pair of setæ. In this connection Professor Hubrecht's[1] inter-

[1] "The Nephridiopores in the Earthworm," 'Tijdschr. Ned. Dierk. Ver.,' ser. 2, vol. iii, p. 226.

esting discovery of the course of the nephridial tube in certain species of Lumbricus (or Allolobophora) will occur to the reader. The facts discovered by Hubrecht, which I can confirm by my own experience, seem to be analogous to those described here. In those worms Hubrecht found that the nephridial duct, after entering the body-wall, passed along it between the two muscular layers to the opening, which is situated in some cases beyond the outer pair of setæ; there is, however, no question, in Lumbricus, of an integumental plexus. Still it is possible that there may be in this peculiar disposition of the nephridial duct in some Lumbricidæ a resemblance to the Eudrilidæ. We may have here a clue to the affinities of the Lumbricidæ, which has been hitherto wanting; but I do not propose to follow up this matter at present.

Reproductive Organs.—The sperm mass of the 11th segment is, like that of the next segment, apparently not enclosed in a sac. When the worm was dissected the mass of sperm could be easily disturbed by the dissecting needle. There was nothing to offer any resistance to the needle. There is, however, seemingly a functional equivalent of the missing sac. The septum which bound this segment posteriorly is comparatively thin, though thicker than the septa in the posterior region of the body. It is inserted on to the body-wall in the usual way. Just before its insertion a sheet of muscular tissue, of precisely the same thickness and general appearance as the septum, arises from the said septum and passes obliquely forwards, ultimately joining the anterior septum of the segment which encloses the mass of sperm. There is thus formed a chamber which encloses the mass of sperm, but which does not seem to be the exact equivalent of the sperm-sacs of other earthworms. It is well known that in many earthworms the successive septa are bound together by muscular bands running in various directions. This state of affairs is more especially characteristic of the anterior and often thickened septa. It is probable, therefore, that the materials for the formation of the septum above described already exist, and that the sheet of tissue which

bound the sperm mass of the 11th segment anteriorly is to be regarded as a development of these muscular threads. In another specimen, however, this peculiar disposition of the septa was absent.

The spermatothecal pouch of this species is single and median, extending from its opening on the border line of the 12th and 13th segments for three or four segments posteriorly. Anteriorly, also, it extends for a short distance beyond the external pore. This portion of the sac is conical in form, as is shown in the figure (fig. 22). The general appearance of the spermatotheca is closely similar to that figured by Michaelsen for Notykus emini (loc. cit. on p. 1, Taf. ii, fig. 8). The spermatothecal sac is also, as in that worm, without lateral branches, such as occur in Stuhlmannia and form a ring round the gut. There is, moreover, a further point of resemblance to Notykus illustrated in my figure, which may be compared with that of Michaelsen. Round the base of the sac in Notykus are represented in Michaelsen's drawing a pair of small glands lettered "*nt.*" It is described by Michaelsen as "ein kleines muskuloses Polster . . . . wahrscheinlich mit einem Hohlraum versehen, welcher durch die oben erwähnten spaltförmigen Öffnungen neben der Samentaschen-Öffnung ausmündet." I shall revert to the probable nature of these organs later. The anterior part of the spermatothecal pouch which lies in the 12th segment is histologically different from the region which it precedes. There is in this particular a remarkable analogy between these sacs which function as spermatothecæ and the true spermatothecæ of, for example, the Perichætidæ. In the latter the diverticula of the spermatothecæ have invariably a different structure from the pouches of which they are diverticula. This, it will be noticed, is also the case with the spermatothecal sac of the present worm. When the sac is examined by a series of transverse sections, from in front backwards, the first pair to appear in the series is of course the anterior diverticulum already referred to. This (fig. 23) is seen to have a circular form in section, and it presents a most curious resemblance to a

section through the œsophagus of a worm. Its walls are muscular and stout. They are lined within by a layer of darkly staining cells which have much the appearance of a low columnar epithelium; the lumen, however, is not simple. Numerous folds of the lining membrane are visible, which project far into the lumen, and nearly meet in the centre. These folds have a fairly regular arrangement. They are not only folds of the lining epithelium, but also of the strong muscular layer. This anterior diverticulum gradually passes into the bursa. The latter is a somewhat flattened sac, with strong muscular walls. It is lined by a regular columnar epithelium. This epithelium is markedly different in appearance from the epithelium lining the diverticulum of the spermatothecal sac; the two layers do not in any way pass into each other. In a series of sections the epithelium of the pouch terminates more or less abruptly; near to its end it gets to be covered by the cells of the diverticulum, which ultimately replace it. In a series of sections quite complete through the anterior of the two genital pores it was impossible to find any external aperture. This was also the case with a second series. Both worms, it should be said, were sexually mature. The epithelial lining of the pouch already referred to dips down towards the epidermis. Some little way above the epidermis it ends abruptly, and the lining of the sac is made up of cells of a quite different appearance. There is, however, no communication that I could discover between the inside of the bursa and the exterior of the body. A moderately thick layer, chiefly cellular, blocks the spot where the aperture should be. The principal part of the spermatothecal pouch lies behind the aperture. At first the pouch is lined with epidermic cells entirely similar to those which line the bursa. These cells form numerous folds in the interior of the sac. The folds, however, are not, as in the anterior diverticulum, supported by upgrowths of the muscular layer. Further back still the folds die away. At first, as already said, the pouch is lined by cells which resemble those of the bursa, and must be, I should imagine, formed by an ingrowth of the epidermis.

These cells are in places partly covered by isolated groups of cells much smaller than themselves. These cells lie to a great extent loose in the cavity of the spermatotheca; only here and there are they congregated into little heaps covering the epidermic lining of the pouch. Presently the covering of peritoneal cells gets to be closer, and coincidently with this the cells which they cover diminish in height, though they are still clearly separated from each other; indeed, the separation is usually marked by a darkly staining but structureless layer, which seems to be thrown off by the epidermic cells. The peritoneal cells which cover the subjacent epidermis are long and filamentous cells, which proliferate freely at their free extremity. The whole structure of the spermatothecal sac of this species seems, as in the case of Eudriloides Cotterilli, which it greatly resembles, to indicate that it is formed out of a peritoneal sac into which an epidermic invagination has grown. The fact that there seems to be no external pore is very remarkable and unintelligible. It is a further point of agreement with the other species of this genus described in the present paper, and also with Stuhlmannia. All the worms that I examined were sexually mature, but in no one of them were there any bodies of any sort within the spermatothecal sac, except the detached cells evidently derived from the lining peritoneal epithelium. In no one of them was there any pore leading to the exterior. It is, of course, possible that at stated seasons there is a pore which is at other times blocked; but this is only supposition, and I have no facts which suggest any interpretation of the use of these sacs. In front of and behind the point where the external aperture of the spermatothecæ ought to be, were it visible, is a glandular mass lying upon the bursa. This mass reaches down on either side, thus forming two rings, one anterior and one posterior, nearly enclosing the spermatothecal sac. These two ring-shaped glands are composed of small nucleated cells, which above the spermatotheca are arranged in a continuous mass. As the gland comes to lie at the sides of the sac its cells become arranged in a series of columns, which anastomose here and

there. In transverse section these columns are seen to be formed of about eight or ten cells whose nuclei lie peripherally. I could not detect any lumen for the most part. In places a lumen appeared to exist. Each disc of cells (as seen in transverse sections) is enclosed in a delicate sheath not closely adherent to the cells. These rows of glandular cells appeared to open on to the exterior, but their external apertures were not very evident. They were plainer in Eudriloides Cotterilli. Glands in the neighbourhood of the spermatothecal orifices are common in the Oligochæta; but the form of these glands in the present species is unlike that which I have seen in any other, excepting, of course, in the other species of the same genus described in the present paper. It may be that Michaelsen's Notykus is furnished with similar glands. The figure given by him seems to indicate a similarity.

The atrium (see fig. 2) differs in structure from that of Eudriloides Cotterilli in the fact that the muscular layers surrounding the glandular lining are thinner; but, though thin, both layers are there. The cellular lining of the atria resembles that of other Eudrilids and of nearly all other earthworms in being composed of two layers of cells. The layer immediately abutting upon the lumen is composed of columnar cells. In certain tracts of the atrium near to the external orifice this layer of cells is very plain, and resembles such columnar cells as line the sperm-duct and their funnel, &c. Elsewhere the inner lining of the atria consists of cells which are loaded with granules, and of which the nucleus has got obscured. The sharply marked layer of epithelium referred to is furthermore remarkable by the presence of cilia. Cilia are also visible in other parts of the atrium, but more obvious along this tract of unmodified epithelium referred to. I believe that this is the first record of ciliation of the atrium in any earthworm. The sperm-duct comes to lie within the muscular sheath of the atrium as in other Eudrilids, but I have not ascertained the exact spot at which it opens into the lumen.

The terminal pouch of the male efferent system is furnished

with a rather complicated arrangement of muscular bands. These are illustrated in the accompanying figure (fig. 21). Just behind the muscular bulbus arise by a common stalk the two atria. At the angle on either side of their entrance into the terminal bulbus is a bundle of muscular fibres running transversely to the longitudinal axis of the body. These muscular fibres appear to be mainly concerned with the penial seta, which is enclosed by them. From each of these bundles of fibres arises a flat strap-shaped band of muscles, which passes forwards obliquely and is inserted on to the body-wall just in front of the edge of the muscular bulbus. Besides these muscles, a number of delicate fibres pass from the parietes to be inserted round the periphery of the bulbus. The latter muscles are, I take it, retractors, while the single strap-shaped muscle on each side, perhaps, by its action when contracted, protrudes the bulbus by drawing back the body-wall just in front of it.

The penial seta of each side of the body lies, as already stated, in the mass of muscles lettered in my figure. These setæ are very strong and rather short, in fact very short if compared, for example, to those of Eudrilus Cotterilli. They are strongly curved into an S-shape, and are a deep yellow colour. The free extremity is not at all ornamented, but it thins off like the blade of a knife, and on this thin edge a few transverse striæ are to be noticed. The genital setæ of this species are decidedly peculiar in form and very characteristic of the species.

Pareudrilus stagnalis, n. g., n. sp. (fig. 9).

I have had for examination a considerable number of individuals of this worm, which is referred to a new genus. It presents upon a casual inspection all the characters of the genus Eudrilus, to which genus I was at first disposed to assign it. Not only are the colour and general appearance quite similar to those of that genus, which also appears to exist on the east coast of Africa, but the position of the reproductive pores are identical, and they are paired—a character which is

only known in the genus Eudrilus, and in the not very nearly allied Nemertodrilus. Nevertheless, a more detailed study of the worm has convinced me that it is an entirely distinct genus, showing, except for the paired apertures of the generative ducts, no particular likeness to any Eudrilus with which I am acquainted. It is probably true that the genus Eudrilus requires revision. It is possible that the individuals from Africa, America, New Zealand, &c., differ specifically among themselves. I confess that I have not been able to detect any such differences, and I am at a loss to understand by what characters Dr. Horst distinguishes his Eudrilus jullieni, though I admit that he only creates the new species in a very diffident manner. On the other hand, Michaelsen's Eudrilus pallidus is, in my opinion, unquestionably a distinct form. These two species of Eudrilus and Nemertodrilus griseus are at present the only Eudrilids with paired genital pores. These Michaelsen places in a distinct sub-family from the members of the family, the great majority of which have median unpaired pores. I shall attempt to show in the sequel that this character is not alone sufficient to distinguish two such groups; that the resemblances between the genus Pareudrilus and certain genera of the sub-family Teleudrilini is closer than that which obtains between Pareudrilus and Eudrilus.

The colour of this worm is a dark purplish brown upon the dorsal surface, becoming light below. The colour was not well preserved in specimens that had been treated with Perenyi's solution. In a single individual, which was brought home alive and preserved by myself in gradually increasing strengths of alcohol, the colour was very dark, as dark as during life; it was much bluer than the rest. All the specimens were found either in the mud at the edge of a pond on Mombasa Island or from a bog up country about four miles from the coast line opposite to Mombasa. The length of a worm selected for measurement was 63 mm., the breadth 4 mm.; this represents about the average size. The prostomium is continued for a short distance on to the peristomial segment by two grooves enclos-

ing a narrow space. The setæ are strictly paired, and ventral in position; the last segment of the body had four pairs just like those of any other segment. The only modification of the setæ that I could see was that the ventral setæ of Segment XVII were wanting, being here replaced by the large penial setæ.

The male pores are paired. They lie on the border line of Segments XVII/XVIII. In one or two specimens a round mass was protruded from the pore which I take to be the partially protruded bulbus atrii. The male pores are on a line with the ventral setæ.

The spermatothecal pore is on the border line of Segments XIV/XV. The clitellum I am unable to place. The only specially noteworthy matter to be recorded about the epidermis is that there is no trace whatever of the peculiar sense bodies, so like the Pacinian corpuscles of Vertebrates, and so commonly met with among the Eudrilidæ. The circular muscular layer can be seen in longitudinal sections to show a decidedly bipinnate arrangement of its fibres; these are grouped into narrowish tracts which are two to four fibres wide. The fibres of the circular muscular layer are laxer in their packing than the longitudinal layer. The interspaces are filled up by delicate strands of an appearance like that of connective tissue. The pigment is chiefly lodged in this outer layer of muscles. It is disposed in tracts that follow the direction of the fibres. Here and there threads of pigment pass down through the longitudinal layer following the course of the blood-vessels. These are so regular in their arrangement that the longitudinal muscular layer is divided up by them into a series of squarish blocks. The peritoneum lining the walls of the body is also pigmented, and pigment also occurs in the peritoneum covering the septa.

The body-cavity contains in parts numerous corpuscles.

The septa are, as in so many, if not in all, earthworms, not attached to the parietes entirely along the grooves which correspond to the external metamerism. The first septum divides Segments V/VI. It is very delicate. The next six are thick-

ened, but not so greatly as is so often the case. The next septum is also thicker than those which follow, but not so thick as those which precede it. All these thickened septa lie behind the gizzard. The anterior septa are cup-shaped.

The alimentary canal is differentiated into a gizzard which lies in the 6th segment. It is long and rather narrow. The œsophagus which follows extends as far as the 17th segment. It is very vascular throughout its whole length, and the lining membrane is so folded that in cross sections the edges look like a mass of tubes containing blood and cut across. The œsophagus is entirely unprovided with glands of any kind appended to it. The intestine has a very small typhlosole.

The nephridia are paired structures. Those of the posterior segments are, as is the general rule, much more obvious in dissections than the few most anterior. This is due to the development of the peritoneal cells which clothe them. These cells are often filled with quite large lumps of an amorphous secretion which stains darkly in borax carmine. It is these secretions which give the white colour and therefore the conspicuous appearance to the nephridia in the posterior segments. When the worm was examined with a hand lens, or even mounted in glycerine on a slide and studied with comparatively high powers of the microscope, there was no indication of nephridiopores. These are usually conspicuous in the Eudrilidæ, but they were absolutely invisible in Pareudrilus.

The reason for the apparent absence of nephridiopores was revealed by an examination of transverse sections. In such preparations the duct of the nephridium could be easily traced into the body-wall in the region of the ventral pair of setæ; the duct of the nephridium was quite obvious on account of its considerable width, and the fact that it has an intercellular lumen. Directly it penetrates the body-wall it becomes of less calibre, and instead of opening on to the exterior forms a duct which runs right round the body-wall on the boundary line between the two muscular layers, and in immediate proximity

to the principal nerve. I have in many cases followed out these ducts to the dorsal mid-line. I am inclined to believe that there is a connection between those belonging to the nephridia of opposite sides of the body. In any case the connection below the nerve cord seems to exist, the duct as it enters the circular muscular layer dividing into a right and left half. The arrangement of the nephridia of this worm is very similar to that which characterises the genus Libyodrilus, but in Libyodrilus there are not only numerous branches of the circular ducts which lead to the exterior, but numerous branches which lead in other directions, thus forming a plexus of tubes within the body-wall. In the present species I did not observe anything of the kind. In one case I found a branch apparently leading to the exterior. Such branches cannot, I am convinced, be very numerous or they would have been more obvious; on the other hand, fine tubes would be very difficult to detect without a special mode of demonstration, and it seems likely that the present species has more resemblance to Libyodrilus than I have at present been able to discover.

The vascular system has not been studied in great detail. In the intestinal region the dorsal vessel gives off three pairs of branches in each segment. The vessel itself lies upon the chloragogen cells, and is covered superiorly by a layer of thin cells, which are not continuous with those of the intestine. Here and there are delicate muscular strands, two or three fibres wide, attaching the dorsal vessel to the intestine; they pass from the muscular layer of one to the muscular layer of the other. There are six or seven of them on each side in each segment. The openings into the dorsal vessel of the branches are guarded by valves. Two pairs of vessels supply the intestinal walls, the third pair spread out over the septum.

Reproductive organs.—Unfortunately there was only a single specimen out of the ten or a dozen examples collected for me that was sexually mature. In this individual the generative organs were dissected, parts of them being investigated later by the section method.

The ovaries were not seen in this specimen, but I have found that they occupy the normal position in the 13th segment. Apparently they are enclosed in a large sac which extends from the septum bounding the 11th and 12th segments. This sac (see fig. 9) is somewhat pear-shaped; it gradually narrows to a fine tube which opens into the large spermatothecal sac. The latter opens on to the exterior between the Segments xiv/xv. The pear-shaped sac, which I believe involves the ovary, is the "ovarialblase" of Michaelsen. A narrow and short tube leads from it to the egg-sac, which occupies the usual position attached to the anterior wall of the 14th segment. From the egg-sac leads another tube, which appears to open into the ovarian sac. This tube, as I have ascertained from a continual series of sections through the entire apparatus, only lies within the ovarian sac; its lumen does not communicate with that of the ovarian sac; the tube soon issues again from the sac, and opens on to the exterior by the oviducal pore. The first tube mentioned which connects the egg-sac with the ovarian sac is really a portion of the funnel of the oviduct—that portion which in other Oligochæta does not open into the egg-sac, but freely into the cavity of the 13th segment. As in the present species, there is a sac developed which involves the ovary; it must happen that the funnel partly communicates with the sac in question. As the latter grows a stretch is put upon the funnel which grows out in the way that we see. The spermatothecal sac is a large pouch which is somewhat bilobed at its free extremity. This region lies posteriorly to the end which opens on to the exterior. In sections it is seen to be lined by an epithelium which is columnar in form, and shows no signs of that proliferation so frequently seen in the spermatothecal sacs of these Annelids. Its interior is folded.

The male organs of generation are as in many other Eudrilids. There are two pairs of testes situated in Segments x and xi; the sperm sacs are in Segments xi and xii, and, like the testes, are attached to the front walls of their segments. The sperm-ducts retain their distinctness until their point of

opening into the atrium. The atria lie perfectly straight on each side of the body; they are comparatively short, and are not twisted as is so frequently the case with the longer atria of other species. Each atrium consists of two parts; the external pore leads into a nearly spherical and very muscular bulbus; from this arises the atrium proper. This tube is quite as wide as the terminal bulbus, and has a nacreous appearance. This appearance is of course due to the stout muscular walls of the organ. In longitudinal sections the atrium is seen to be composed of four layers exclusive of the peritoneum; beneath the peritoneum is a layer of longitudinally disposed fibres; beneath this, again, a layer of circular fibres. These two layers are of about the same diameter. The lining membrane of the atrium is built up of two strata of epithelium; the innermost layer is composed of not very tall columnar cells, outside which are several layers of slightly staining pear-shaped glandular cells. The two layers of epithelium together are twice as thick as the muscular coats.

Each atrium is accompanied by a long, thin, muscular sac, which is nearly, if not quite, as long as the atrium itself. This sac is placed to the outside of the atrium, and is slightly curbed. Each of the two sacs contains a single very long penial seta. It is very thin, and curved more sharply at the free extremity. The free end of the seta expands at the actual extremity into a thin, flattened plate; just before this the seta is beset with a few short spinelets.

I have been able to study the female reproductive system in immature worms, and to ascertain that the spermatothecal apparatus is formed from at least two sources. The spermatotheca appears to be formed by an epidermic invagination. Its lining epithelium is continuous with the epidermis. This sac is large and has very thick walls. It appears at first sight to be independent of any other part of the system and I believe that originally it is so. However, in all the specimens examined by me there is a strand of tissue, principally constructed of muscular fibres, which has in the immediate neighbourhood of the spermatotheca no lumen. This

solid strand joins the spermatotheca. Traced in the opposite direction it is seen to gradually develop a lumen, which gets wider and wider until it expands into a trumpet-shaped orifice which opens into the 13th segment. It seems in fact to be clear that this tube, which ultimately forms the communication between the ovary egg-sac and spermatotheca, is merely a backward growth of the septum separating Segments XIII/XIV. The oviducal funnel lies just above the mouth of this diverticulum of the septum, and is placed within the mouth of the egg-sac. The oviduct itself, shortly after it expands to form the funnel, projects into the interior of the septal sac; it does not open into it, but is enclosed by the walls of the said sac. At this stage the ovary is quite free, and is attached in the usual position to the anterior septum of the 13th segment.

The development of the corresponding regions of the female generative apparatus has been studied by myself in Libyodrilus violaceus; I was able to show that nearly the whole of the large spermatothecal sac originated from the cœlom, the septa being modified to form its walls; at most the merest trace of an invaginated part was to be found at the external orifice. I suggested that the large spermatothecal sacs of Eudrilus and Teleudrilus were also probably to be regarded as the homologues of the unpaired sac of Libyodrilus. The facts that I make known in the present paper do not lead me to adhere to that opinion. For in Pareudrilus it seems to be more than probable that the whole of the spermatothecal sac is an invagination, and that the egg-conducting apparatus only is of mesoblastic origin, and has a cavity which is an enclosed section of the cœlom. The nature of the spermatothecal sacs of the Eudrilidæ was first proved by myself to be different from that of other earthworms in the paper upon Libyodrilus referred to; at least it was rendered exceedingly probable that the conditions obtaining in Libyodrilus were not confined to that genus, but were characteristic of the whole group. Rosa, however, independently in point of observation, but subsequently to myself in date of

publication, arrived at the same results. His results, however, were not the outcome of a study of the young stages, but of a comparison of the structure of the several regions in the adult. He found that the epithelial lining of the sac stopped abruptly at a point not far removed from the external aperture, and gave place to a layer of cells of an entirely different character, and like the peritoneal epithelium. It may, I think, be regarded as certain that a great part of the complicated system of spaces surrounding the ovary, and communicating with the exterior, in the Eudrilidæ are derivatives of the cœlom, but it is also clear that a variable tract of what has been termed the spermatotheca is really an invagination of the epidermis, and is therefore comparable to the spermathecæ of other worms. I shall recur to this subject in describing the anatomy of some species of Eudriloides. The development of the sac *a* shows how the oviduct comes to be partly enveloped by it; as it is simply a part of the cœlom, there is nothing to be surprised at in the fact that the oviduct lies within it.

§ Affinities of Pareudrilus.

This genus evidently is referable to the second of the two sub-families into which I divide the Eudrilidæ (see below). It has no integumental sense-organs of the characteristic form found in Eudrilus and other allied genera. The spermducts are not dilated at their junction with the funnels. There are no calciferous glands. It is the only genus in this sub-family besides Nemertodrilus which has paired reproductive apertures. A very marked peculiarity of the present genus is arrangement of the nephridia. This is only paralleled, so far as we know at the present time, in the West African genus Libyodrilus. In that genus there is a complex system of integumental nephridial tubes. Nevertheless it is not perhaps the only other genus in which this peculiarity occurs. In the description given by Michaelsen of Megachæta tenuis, it is stated that the nephridiopores could not be discovered; so, too, with Notykus and Metadrilus.

In the latter genus, however, Michaelsen was unable to see the nephridiopores, but found (by transverse sections) that the nephridiopores were placed in the neighbourhood of the ventral setæ. It seems to me to be possible that in these species there are nephridia of the type which characterise the genera Libyodrilus and Pareudrilus. When the nephridia are of the usual form, the orifices are so conspicuous that it is almost impossible to overlook them. In these three genera, moreover, as well as in Libyodrilus, the atria are comparatively short and have very muscular walls. These are additional points of resemblance to Pareudrilus. Pareudrilus differs from Libyodrilus mainly in the form of the female reproductive apparatus, and in the absence of the three posterior gizzards. With Metadrilus, the genus Pareudrilus agrees in the position of the spermatothecal orifice. But in Metadrilus the spermatothecæ are much reduced, and there are besides only the rudiments of penial setæ. The affinities of Pareudrilus are with the genera mentioned, but no one of them can be said to be much nearer than the others.

Polytoreutus violaceus, n. sp. (figs. 3, 7).

Two species of the genus Polytoreutus have been at present described. The type species of the genus, P. cœruleus, was described briefly by Michaelsen in a preliminary account of the earthworms of Zanzibar and the opposite mainland,[1] and subsequently re-described in a more thorough fashion.[1] A second form, P. magilensis, was afterwards described by myself from Magila, East Africa.[2] I have now to add a third species, which I name P. violaceus, on account of the colour of the worms.

There were four examples of this species in the collection; all of them were fortunately sexually mature, and all of them were about the same size. The length of one individual which was selected for measurement was 83 mm., its diameter 4 mm.

[1] Loc. cit. (on p. 201).

[2] "Some New Species and Two New Genera of Earthworms," 'Quart. Journ. Micr. Sci.,' vol. xxxiv.

The species is therefore fairly stout in build. This individual had 190 segments. The size of the species is therefore about the same as that of Polytoreutus cœruleus, and considerably less than that of P. magilensis.

The dorsal surface of the preserved specimens was of a reddish purple, bluer perhaps in some than in others; but there was nothing that could be fairly described as "leuchtend himmelblau," a term which Michaelsen uses in writing of Polytoreutus cœruleus. The under surface was yellowish. The clitellum also was readily distinguishable from the rest of the body by its yellowish coloration. The coloration of this species was indeed almost, if not exactly, that of the genus Eudrilus.

The prostomium is broad and does not indent in the least the buccal segment. This is a generic character, and not peculiar to the present species.

The clitellum occupies Segments XIV—XVIII or in some specimens XVII only. It is less developed on the ventral than on the dorsal or lateral surface, and it is here only that the boundaries of the segments, which compose it, are clearly visible. The clitellum may in fact be spoken of as "saddle-shaped," though there is really no distinction to be drawn between a clitellum of this kind and a "cingulum." In both the remaining species of the genus the clitellum has been described as complete, and consists of an additional segment, the 13th.

The nephridiopores are lateral in position.

The setæ are paired, and are nowhere deficient except upon Segment XII (see below). The two setæ of each of the ventral pairs are, however, further apart from each other than are those of the lateral pairs. This arrangement was apparent on the posterior as well as on the anterior segments of the body; it is not peculiar to the present species, but also characterises P. magilensis and P. cœruleus. Michaelsen found no setæ upon the clitellum of the last-mentioned species; they were certainly not absent from this region of the body in Polytoreutus violaceus.

The median genital pores lie, as in the other two species,

on Segments xvii—xix. The middle region of the 18th segment is occupied by a protuberant swelling of the body-wall, which also extends for a short distance on to the segment in front; this lies entirely between the ventral setæ. The posterior border of this projection appears to be the boundary line of Segments xviii/xix. Anteriorly, however, the border line of Segments xvii/xviii is seen to end on each side behind the anterior part of this protuberant pad. The anterior orifice therefore lies on the 17th segment, and not on the border line between this segment and the one which follows. On the other hand, the posterior aperture, which is that of the spermathecal pouch, is distinctly on the border line of Segments xviii/xix. The latter orifice appears to be very much smaller than the male pore, which has slightly crenated lips. The ventralmost seta of Segment xvii is absent on both sides of the body. The present species is also remarkable for a median unpaired papilla situated upon Segments xxii and xxiii. This is oval in form, and is flattened with a raised margin. It commences at the level of the setæ of Segment xxii, and extends back as far as the end of the next segment, the border line of which convex backwards. The median region of this segment is, in fact, very much wider than that of the neighbouring segments. The ventralmost seta of Segment xxiii lies on the papilla on both sides of the body; on the 22nd segment that seta of the left side is upon the papilla.

Reproductive Organs.—As in other species of the genus, Polytoreutus violaceus has only a single pair of testes. These lie in the 11th segment; they are not, however, attached to the front wall of their segment, nor are they, as is sometimes—though rarely—the case with earthworms, attached to the posterior wall. They are attached to the wall of the sperm-sac, which commences in this segment. It can hardly be doubted that originally the testes were attached to the front septum of the 11th segment; but the growth of the sperm-sac appears to have cut them off from this position, and in the adult worm the heart lies between them and the septum in question. The testes lie in the proximal end of the sperm-

sac. The sperm-sacs are paired, and extend, as in *Polytoreutus magilensis*, through a large number of segments. Their commencement is in the 11th segment, and here they are somewhat dilated. The upper wall of the sperm-sac curves round, and is attached to the dilated part of the sperm-duct, the testes lying just in the angle formed by it and the wall of the sperm-duct dilatation. The lower wall of the sperm-sac is formed by the septum separating Segments XI/XII. The sperm-sac then perforates this septum, and becomes a very narrow tube not more than a quarter or less of its dimensions at first. These two fine tubes pass along the dorsal surface of the gut side by side, and in contact with each other. They are partially concealed from view by the bulky atria, which also lie—at least for the greater part of their course—upon the dorsal lateral aspect of the intestine. At about the 30th segment of the body the two elongated and narrow sacs appear to fuse together and form a much wider sac, which extends back for about ten segments, and is deeply constricted at the points where it passes through the intersegmental septa. The atria are circular in section. The lining epithelium is, as usual, composed of two kinds of cells; it is much folded. The muscular layers are excessively thin. On the lower surface of the atrium, but within the muscular coats, run two blood-vessels, between which is a distinct thickening of the longitudinal muscular coat. The two atria fuse together before opening on to the exterior. The exact point where the sperm-duct enters the atrium I have not discovered, but in any case it is not at a very great distance from the external pore.

The illustration (fig. 7) will give some idea of the very remarkable character of the spermatothecal sac. It extends through five segments—from its beginning in the 14th to its external aperture on the border line of Segments XVIII/XIX, and for two segments beyond this point—to the 21st segment, in fact. The spermatothecal sac is single, but shows unmistakable indications of being the result of a fusion between two originally separate sacs. Anteriorly it is in contact with the wall between Segments XIII/XIV. There are two diverging

horn-like processes which meet in the middle line of this segment. They end blindly in front. Just at the blind end the egg-sac is attached to each whence the oviduct passes outwards, as shown in the figure referred to. The median sac formed by the fusion of the two anterior sacs passes straight down the body-wall below the ventral blood-vessel and the nerve cord. It is a narrow tube, but is rendered conspicuous by the fact that it gives off on either side a series of diverticula. These diverticula are accurately symmetrical. They are narrower at their origin from the median sac, and become dilated at their free end, which is of course closed. Their shape reminds one of the Polian vesicles of the Holothurians. In another specimen, also mature, which I dissected, these lateral vesicles showed an asymmetry. Those of the left side were, with the exception of the fifth, much smaller than those of the right side. I regard this as an abnormal or perhaps, in spite of appearances, not a fully mature specimen. These lateral cæca of the spermatotheca bore a distinct relation to the metamerism of the body; there were, in fact, a pair of them to each segment. The atria pass between the fifth and sixth pairs. The two last pairs are beyond the aperture of the spermatotheca. The most anterior pair of diverticula—those which bear the egg-sacs—differ from all the rest in being a little longer and narrower. I have investigated the minute structure of the spermatothecal apparatus in this species by longitudinal sections. The first point of importance to be noted is that they contain spermatophores exactly like those of Polytoreutus magilensis, a species recently described by myself in this Journal.

These spermatophores do not for this reason need any particular description. Their distribution, however, is remarkable. They do not, as perhaps they might have been expected to do, occur in the entire spermatothecal sac. They are restricted to the end of the sac, which, as already mentioned, lies in the 13th segment. These two sacs at the end of the spermatothecal sacs are crowded with spermatophores. I have also seen spermatophores at the external pore of the spermato-

thecal sac, but never in between. I find it difficult to understand this. The spermatothecal apparatus is so large that it must, one would think, perform some function not performed by spermatothecæ which are smaller in size; for instance, those of Eudrilus. The presence of spermatophores needs more room, supposing that there is about the same amount of sperm. But the restriction of the spermatophores to the anterior end of the spermatothecal apparatus is still unexplained. In Polytoreutus cœruleus and in Polytoreutus magilensis the oviduct is dilated near to the opening into the egg-sac. In this dilatation are lodged bundles of sperm. Michaelsen has suggested that this looks as if the ova were fertilised in the egg-conducting apparatus. The facts described in the present paper support this contention, but unfortunately throw no further light on the exact place where fertilisation takes place. The spermatothecal sac is lined throughout with a layer of very tall columnar cells, the nuclei of which are near to the attached base of the cells. In the anterior part of the spermatothecal sacs where the spermatophores are lodged these latter are seen to lie partly among the cells, having, as it were, thrust their way in between them. There were, however, no indications that the cells lining the sacs are in any way responsible for the formation of the spermatophores.

The ovaries of Polytoreutus cœruleus have been described by Michaelsen as lying in a spherical chamber which itself lies at the extreme end of each of the two branches in which the spermatothecal sac ends anteriorly. The epithelium lining this chamber is believed by Michaelsen to be the ovarian epithelium. This spherical pouch is attached to the Septum xii/xiii by a strand of connective tissue. In Polytoreutus violaceus the position of the ovarian chamber—if I am right in so calling it—is rather different. At the point where the large terminal chamber of the spermatothecal pouch comes nearest to the Septum xii/xiii there is a minute sac attached to its wall, and formed of a muscular coat with a lining of epithelium. Where this sac is in contact with the wall of the spermatothecal sac there is no development of muscles, so

that the epithelium of both pouches is in actual contact. This minute sac is attached to the Septum XII/XIII by a strand of fibrous tissue (muscular or connective tissue). It is situated on the opposite side of the spermatothecal sac to that on which is placed the orifice of the duct leading from the oviduct. The sac was filled with a few small rounded cells which might be immature germinal cells or might, indeed, be any kind of cellular tissue in an immature state. I have no evidence to bring forward that this tissue is really what is left of the ovary, except its position and the fact that it is enclosed in a special sac.

The egg-sac and the oviduct appear to have the same structure and relations as in Polytoreutus cœruleus. The only difference that I noted was the absence of any diverticula of the oviduct lodging sperm masses such as Michaelsen has figured and described in that species. The egg-sacs contained, besides ripe ova, germinal cells in various stages of growth.

In describing the structure of Polytoreutus kilindinensis I shall have some observations to offer about the development of the different parts of the female reproductive organs.

Polytoreutus kilindinensis, n. sp. (fig. 8).

The present species was represented by two individuals, both of which were collected at Kilindini, on Mombasa Island; they were found, together with another species to be presently described, in damp ground where the slops of a household were deposited.

This species cannot be confounded with the next, nor with either of the two remaining species of the genus. It is larger than the last; the larger of the two individuals measures 120 mm. in length by a diameter of 5 mm. This specimen consisted of 220 segments. The colour, too, is different; it is characterised by the same general coloration, but the violet is less deep and less extensive.

The prostomium is broad, and does not invade in the least the buccal segment; the latter segment has numerous wavy lines anteriorly.

The setæ seem to be as in other species of the genus. There seems to be a tendency for the ventral setæ to be defective upon the segments which bear the genital pores; I refrain, however, from giving any details, since I am not certain how far this deficiency may be normal.

The nephridiopores are lateral in position.

There is no median genital papilla such as occurs in P. violaceus.

The clitellum extends over Segments XIV—XVIII, being only developed upon the anterior half of the last segment. Behind the clitellum is a median area bounded by the ventral setæ, which looks like an extension of the clitellum; it has the same tumid appearance, and the boundary lines between the segments are there not apparent. This area reaches from the 18th to the 21st segments; when the worm is seen in profile it is seen to project somewhat. It is very possible that this area serves the purpose of the genital papilla in Polytoreutus violaceus.

The anterior of the two median and unpaired genital openings is situated on the border line between Segments XVII/XVIII; it is a widish aperture with crenated margins; behind it is a transverse groove which runs for a considerable distance right and left; this groove is not, as might be supposed, the boundary line of Segments XVII/XVIII; it can be easily seen that the furrow between these segments is anterior to it and bisects the genital pore already described. Immediately behind the groove referred to is the posterior genital aperture; this is much less conspicuous than the anterior pore, and has not crenated margins.

The internal structure of this species is very similar to that of the last, but there are certain recognisable differences. There are six specially thickened septa; the first of these lies behind the 5th segment, and the last behind the 11th segment. As appears to be usual in the family Eudrilidæ, these septa are not much connected together by threads.

The gizzard lies in the 5th segment, and is small; the calciferous glands, of a white colour, are in Segment XIII; the

unpaired calciferous pouches are in Segments IX—XI, and are reddish in colour.

Reproductive Organs.—The sperm-sacs are, as in the other species of the genus, long, but they are by no means so elongated as in Polytoreutus magilensis; they commence in the same way in the 11th segment, and are at first thin tubes; in the next segment, however, they attain their ultimate size, and extend back to about the 27th segment. The two sacs run close together on the dorsal surface of the intestine, but they do not become fused as is the case with Polytoreutus violaceus; the sacs are constricted where they pass through the segments; their whitish colour contrasts with the orange colour of the atria, which extend through the same segments that they do.

There is a single pair of sperm-ducts which open into the 11th segment; they show the usual dilatation before their opening; the atria present no noteworthy particulars; they extend as far back as do the sperm-sacs. It is in the disposition of the spermatothecal pouches that the present species is chiefly to be distinguished from its congeners.

Fig. 8 illustrates the arrangement of the sacs. From the point of opening on to the 17th segment a narrow median tubular sac passes forwards beneath the nerve-cord up to the 14th segment; here it divides into two sacs, each of which immediately becomes dilated into a wide pear-shaped pouch lying transversely to the longitudinal axis of the body; just where this pouch narrows into the stalk which connects it with the median spermatothecal sac a short tube arises, which very soon dilates into the funnel of the oviduct; the latter is a globular sac, as in other species of the genus, and is connected on the one hand with the oviduct, and on the other with the egg-sac, as is shown in the figure. I could find no spermatophores in the sac—not the least trace of the bundles of spermatozoa figured by Michaelsen (Taf. iv, fig. 30, sk.), and observed by myself in Polytoreutus magilensis, were to be seen in the present species.

The spermatothecal sac of the present species is the simplest that has yet been met with in the genus. The appendices of

the median sac, that occur in the remaining species, are here quite absent; the storage of the sperm is effected by a development, not met with in the other species, of the anterior end of the sac on each side.

I investigated the structure of the female reproductive organs in an immature example of this species. The spermatothecal sac was almost filled by small rounded cells, quite unlike the tall columnar cells which line the mature spermatothecal sac of Polytoreutus violaceus. So numerous were these cells that the lumen of the entire tube was almost completely obliterated. I had hoped to find some indication of the position of the ovary in this specimen; but, unless the epithelium lining the two end pouches into which the spermatothecal sac divides anteriorly is the germinal epithelium, I could find nothing at all. There is not, as there is in P. violaceus, a small sac attached to the main spermatothecal sac, set apart for the lodgment of the ovary. It is probable that the ovary is only free in very young specimens, and it is also possible that it has a very transitory existence. There is a precedent for this in Libyodrilus. In that genus the ovary appears to exist only for a short time, its contents being early transferred to the interior of the egg-sacs. In this young specimen of Polytoreutus kilindinensis the egg-sacs were quite fully developed as regards size, but they contained only quite immature cells; the germinal cells filling the egg-sacs were exactly like the cells in the immature ovary of other worms; it is evident, therefore, that the germinal tissue is transferred en masse to the egg-sac, and that the entire development of the ova goes on in those sacs. The spermatothecal sac seems not to be formed by an invagination from the epidermis; the epithelium lining it bears no resemblance at all to the epidermis; the structure of the sac is exactly like that of the developing sperm-sac which lies in the preceding segment; in the section of the worm the two could be very well compared, as they almost came into contact. Judging from structure only, no one would hesitate to regard the two structures as of the same nature.

§ Note upon an Immature Example of this Species.

From the same locality I have an example of a Polytoreutus which I regard as an immature specimen of P. kilindinensis. It measured 98 mm., and consisted of 158 segments. The external characters, except those afforded by the apertures of the reproductive organs, were as in the species P. kilindinensis. The reproductive openings were only represented by a pore upon the boundary line between Segments XVII/XVIII. This pore was, however, extremely conspicuous, and showed no indications of being in an immature condition. Behind the pore was a short transverse groove such as exists in the mature worm, but there were no signs of the second pore. The internal anatomy, apart from its immature state, showed one or two small differences from that of the species of which I presume the present example to be an immature one. There was a thick septum in front of the gizzard, which, therefore, separated Segments IV/V. The dorsal vessel also was double, a rare condition in this family. The dorsal vessel was formed of two tubes, at any rate in Segments VIII—XII. The two tubes became fused at the septa. There are other examples beside the present which appear to show that a double or a single dorsal vessel is not necessarily a diagnostic character of a species. Thus I described the dorsal vessel of Megascolex cœruleus as double, while Bourne saw no signs of any such doubling. Another point in which the present specimen differs from the type of the species is in the fact that the two sperm-sacs join together at their distal extremity. The median calciferous pouch of Segment XI was distinctly smaller than the two which precede it.

The sperm-sacs, it should be said, are of precisely the same form as in the mature examples; that is, they arise from the septum bounding posteriorly the 11th segment. At first each sac is thin, and this region extends through one segment only. It may, therefore, be pointed out that the probability of this shape of the sperm-sacs being characteristic of the species and distinguishing it from, for example, Polytoreutus magi-

lensis is increased by the fact that the immature worm exhibits the same condition. The funnels of the sperm-ducts were by no means so prominent as in the fully mature worm; they, of course, occupied the same position. The only other part of the male apparatus that was visible were two little sacs lying one on either side of the extremity of the spermatothecal sac. I do not think that these were the immature sacs of the penial setæ of a species of Polytoreutus provided with these structures. It seems, therefore, that the first rudiment of the terminal apparatus of the male ducts is double, which is so far a demonstration that originally this apparatus was double. Beyond these two minute sacs nothing was visible of the male efferent ducts. On the other hand, the spermatothecal sac was as well developed as in the mature worm. It showed no differences that I could detect from the structure already described. There was, however, no sperm in the sac.

We may, therefore, note that the female apparatus is developed before the male, and that the sperm-sacs are the first part of the male apparatus to reach maturity.

Polytoreutus Finni, n. sp. (figs. 6, 17).

I have unfortunately only a single specimen of this worm for examination. It is extraordinarily long and thin—perhaps I may say even for an Eudrilid. The preserved specimen measured 183 mm. by 3 mm. in breadth at the clitellum, which is distinctly broader than any other region of the body. The worm consisted of rather more than 500 segments, a most unusual number. The clitellum is exceedingly conspicuous, being raised above the level of the surrounding segments; it occupies Segments XIII—XVIII. It is quite complete except for the area which lies between the genital pores. The genital pores (fig. 17) are, as is usual with this genus, situated on the 17th, and on the boundary line between the 18th and the 19th segments respectively. These apertures are very large and prominent, and are surrounded by thick tumid lips. The integument at the actual orifice is marked by numerous slight furrows which have a radiate arrangement. These pores,

together with the modified integument immediately surrounding them, occupy nearly the whole of the ventral surface of the worm. Between the anterior and the posterior orifice is a tract of integument of the same character as that which immediately encircles the pores, and differing from the clitellar tissue.

The setæ are as in the other species of the genus.

The internal structure, no less than the external characters, distinguishes Polytoreutus elongatus from the remaining species of the genus Polytoreutus. These differences mainly concern the spermatothecal sacs, which are different in all the species of the genus. In other particulars there is less difference. The last specially thickened septum divides Segments XI and XII. The last pair of hearts are in Segment XI. There are the usual three median calciferous pouches in Segments IX, X, and XI. The calciferous glands are present, but have a very unusual form; they appear to lie in the 15th segment, but I am not able to be quite certain, as the segments just about this region were hard to fix. Not only are the calciferous glands unusual by reason of their position, they are also peculiar in shape. Each gland is situated at the sides of the œsophagus, and is curved up like a ram's horn.

As in the other species of the genus there is but a single pair of funnels; and I presume, though I have not actually verified the fact for the present species, they have only a single pair of testes. The funnels of the sperm-duct lie in the 11th segment, and the funnel itself is preceded by a dilated section of the sperm-duct, which has an opaque white appearance, and is of large size. It is directed obliquely backwards. I have not followed the course of the sperm-duct.

The atria are long; they open together into a terminal bulbus which is median in position, and again opens on to the exterior by the anterior of the two genital orifices already described. The atrium belonging to the right side of the body was extended at full length, while that of the opposite side was looped once or twice. The fully extended atrium reached

back to about the 25th segment behind the clitellum; a peculiarity about it was the fact that the last half or rather less of the gland was double, the two portions, however, running in close contact. Whether, as seems likely, this is a mere abnormality I am unable to say; but I may point out that in Eudrilus each atrium is normally divided into two separate tubes by a continuous longitudinal septum.

The sperm-sacs are very remarkable. On the dorso-lateral surface of the intestine I observed a pair of fine tubes running a fairly straight course, which I put down at first as being the sperm-ducts, thinking that they terminated in the atrium. They do as a matter of fact terminate close to the atria, but quite independently of them. These slender tubes are the sperm-sacs. One of them, that of the left side, was distinctly varicose, being dilated here and there into oval chambers. Traced forwards, they appeared to end in the immediate neighbourhood of the funnels. Each sperm-sac was accompanied by a blood-vessel. It is a pecularity of this genus to possess long sperm-sacs, which in Polytoreutus magilensis are of enormous extent, but in no other species are they of the extreme tenuity exhibited by Polytoreutus Finni. This state of affairs may be simply due to the fact that the sperm did not happen to be present in any great amount; but this is unlikely, as the worm was in all other respects fully mature. Besides, this is not the only case of a worm possessing such extraordinarily long and thin sperm-sacs. I have described elsewhere the sperm-sac of the Geoscolicid genus Trichochæta, which are of precisely the same character as those of the present species of Polytoreutus. On the other hand, it will be recollected that there are a number of different degrees in the development of the sperm-sacs in this genus which may perhaps be interpreted as different grades of development of the sacs. In Polytoreutus magilensis the sperm-sacs are at first extremely narrow, and later become much wider. In Polytoreutus kilindinensis, described on a preceding page of the present paper, the narrow region of the sperm-sacs is reduced greatly, nearly

the whole of the sacs being wide. Finally in the present species we have the other extreme. The entire sperm-sacs are formed by the slender tubes referred to.

The female reproductive organs present a fourth variety, all the species at present known being different in the form of these organs. They are most like those of Polytoreutus kilindinensis. P. Finni agrees most closely with P. kilindinensis in the general form of the spermatothecal sacs. As in the last-named species, there are only a single pair of diverticula of the median unpaired sac. The latter runs beneath the nerve cord until it reaches the anterior boundary of the bulbus of the male efferent apparatus. Arrived at this point it diverges to the left, and, forming a semicircle, again bends to the middle line, and opens by means of a dilated terminal sac behind the orifice of the atria. Anteriorly this median sac extends as far as the 13th segment. Just below the septum which divides this segment from the one in front, it divided into two. Each branch swells out as in P. kilindinensis and forms a largish oval sac. The two sacs are coiled to some extent round the intestine. From the base of each, not far from the point where it joins the median sac, a short tube is given off, which passes into the receptaculum ovorum and thence becomes continuous with the oviduct. The arrangement of these parts is, in fact, precisely as in Polytoreutus kilindinensis. They are illustrated in fig. 6.

Alluroides Pordagei, n. gen. (figs. 4, 5).

I shall describe this new form under the name of Alluroides Pordagei. It was collected along with a number of examples of Stuhlmannia variabilis in a swamp four miles up country, opposite to Mombasa Island. The species is represented by only two individuals, measuring in the preserved state about an inch in length. They had a delicate appearance owing to their small size and the thinnish body walls, and resemble somewhat, except in colour, an aquatic member of the family Phreoryctidæ which I have lately described from New Zealand under the name of Pelodrilus violaceus. In

fact, any one acquainted with this group of worms would probably assign the species from its general appearance to the Lumbriculidæ or perhaps to the Tubificidæ.

Reproductive organs.—The testes are a single pair only, which are placed in the 10th segment attached to the front wall of that segment. There appear to be no actual sperm-sacs, but the 10th and the 11th segments are filled with a mass of developing sperm. This is so compacted together that the appearance of a definite sac is produced, and the sperm is so abundant and occupies so much of the interior of the two segments in question that the septum dividing them, which is thinnish, is hardly visible without a very careful inspection.

The funnels of the sperm-ducts correspond in number to the testes, that is to say there is only a single pair, which lies opposite to the testes in the same segment. They are much folded.

The terminal apparatus of the male efferent duct is formed by an atrium.

The atria (fig. 5) extend through more than one segment, and are long enough to be coiled. They open on each side on the 13th segment, the aperture being lateral in position, showing therefore, which is remarkable, no relation to the pores of the spermatothecæ. The tubular atria have, however, not a close resemblance in structure to the tubular atria of such genera as Acanthodrilus. Their structure is as follows: —The internal lining of the tubes is formed by a single layer of cells, which have a clear appearance, as they were not stained by a long immersion in borax carmine. The cells were certainly in some places ciliated. Towards the external pore these lining cells got to be more and more like the epidermic cells, and were also ciliated, until at the actual orifice they became continuous with the epidermis. Outside the epithelium is a layer of muscular fibres of some thickness. These fibres are entirely circular in disposition. They do not form an absolutely continuous covering of the epithelium; here and there slight gaps are to be seen. These gaps correspond

to the exits of the ducts of a mass of glandular cells which form the outer covering of the organ. As in Moniligaster, the atrium is invested externally by a mass of pear-shaped cells, which are loosely compacted into separate masses.

The structure of the atrium, therefore, is like that of Moniligaster alone among "earthworms." In fact, it only differs from the atrium in that genus in its greater length. The external aperture of the atrium is placed upon a fan-shaped outgrowth of the body wall, which in all probability serves as a penis. Whether or not these penes are in- and evaginable I am unable to say. They were extruded in both the specimens at my disposal. I should imagine that they are protrusible.

The ovaries are in the 13th segment.[1] They are attached as usual to the front wall of this segment. From the 13th to about the 20th, there are ova and masses of ovarian cells apparently lying loose within the body cavity. In the most anterior of the segments in question, there are only egg masses consisting of immature ova surrounded by groups of small cells, but in the segments situated further back, there were only ripe ova visible. These ova are of special interest on account of their large size; they are also, like the ova of the aquatic Oligochæta, generally crowded with yolk. The ova are fully as large as those of such a genus as Rhynchelmis. In longitudinal sections of the body the ova reached across nearly from one side of the body to the other.

I could find no egg-sacs. There is a single pair of oviducts which open into the 13th segment. The tube remains very wide after it has entered the 14th segment, and has a much folded lumen; it narrows rapidly before the external pore.

The spermatothecæ are present to the number of a single pair, which are in the 8th segment. They are oval pouches without any diverticula, and with perhaps unusually thick

[1] The septum dividing Segments XIII/XIV was largely deficient, and masses of young egg-cells and non-differentiated germinal cells passed into the 14th from the 13th segment. I should not like to be certain that these were not developed in situ; younger specimens are required to clear up the matter. In the meantime there is only one pair of oviducts.

muscular walls. They open quite dorsally close to the median dorsal line of each side of the body. This is a remarkable but not unknown position for the spermatothecal pores. Another instance of a similar position, which occurs to me, is in the species Allolobophora fœtida.

Other facts in the anatomy of the worm which are of some little importance are the following.

The prostomium is, as is indeed usual, covered with a thick columnar epithelium. This thickened pad is prolonged for a very short distance into the mouth-cavity. This epithelium is very possibly of a sensory nature. The cœlom is, of course, divided up by transverse septa into a series of chambers. Some of the septa which divide these chambers are thicker than others. The first of these thickened septa divides Segments IV/V. The following seven septa are, with the exception of that which divides Segments X/XI, also thickened. The next septum to the last of the specially thickened septa is rather thicker than the excessively fine septa which separate the following segments. As in so many of the lower Oligochæta, there are septal glands present; these glands commence in the present species in the 5th segment, and the last pair were observed in the 9th. The brain lies in the 3rd segment. From the brain one among several nerves which pass forward ends in a medianly situated ganglion in close juxtaposition to the epithelium of the prostomium, which consists of but few cells. A median ganglion in this position has not, I believe, been described as existing in any earthworm, but it has been met with in certain aquatic Oligochæta belonging to the family Tubificidæ. In this family Stolc[1] has figured such a ganglion in Bothrioneuron and in Lophochæta.

The alimentary tract has no traces of a gizzard. The œsophagus does not appear to be at all vascular; it terminates in the 13th segment, in which segment begins the intestine. There are no glands of any description appended to the alimentary tract unless the septal glands can be referred to this category.

[1] "Monogr. Ceskych Tubificidu," 'Abh. böhm. ges.,' 1888.

The nephridia commence in the 16th segment. They open on to the exterior by the second seta. They are clothed with a thick layer of peritoneal cells.

The question now to be considered is the family into which this new type should be placed. That it is generically distinct there is in my opinion no doubt whatever. This genus Alluroides is one of those forms which render the distinction between the old groups of the "Limicolæ" and the "Terricolæ" untenable. In some respects it is even more perfectly intermediate than Moniligaster.

Aside from Moniligaster, the "waterworms," all of them, differ from any earthworm in the following characters:

1. Clitellum one cell thick.
2. Ova very large and full of yolk, few in number.
3. Genital aperture situated far forwards.
4. Egg-sacs occupy more than one segment.

These are positively all the distinguishing marks if we leave aside the genus Moniligaster. Moniligaster itself, as I have shown in several papers[1] dealing with the structure of this remarkable worm, breaks down the first, third, and fourth of the above distinctions. Moreover, it has eggs which, although they are not greatly above the average size of the eggs in earthworms, differ from those eggs in containing a great quantity of yolk in the form of large spherules. Moniligaster, in fact, is only an earthworm in having a gizzard or rather gizzards, and in the comparative thickness of the body-wall. This latter character, however, is seen in Phreoryctes, which is one of the genera assigned by Claparéde to his division Limicolæ. Besides the points enumerated in the above tabular statement, Moniligaster has various other resemblances to several Limicolous Oligochæta, which are not of first-rate importance from the present point of view, inasmuch as they also occur in other earthworms, though not to so marked a degree. The atrium, for example, is almost exactly like that of the Lumbriculidæ. The protrusible penis is constructed more on the lines

[1] For a list of literature see "Description of New or Little Known Earthworms from various localities," 'Proc. Zool. Soc.,' 1892, p. 690.

of the corresponding organ in the Tubificidæ than is the penis in the Eudrilidæ and other terrestrial Oligochæta which possess an organ of this kind. The atrium is lined by a single layer of cells, a feature which is also found in Ocnerodrilus and in some other genera. The sperm-duct has a very short course, opening on to the exterior in the next segment to that which contains the internal funnel. It is quite possible, however, that Tetragonurus shares this peculiarity with Moniligaster. So, too, with the oviducal pores. Moniligaster is not alone among earthworms in the fact that they are in front of the sperm-duct pores. In both Allurus and Tetragonurus the oviducal pores are nearly certainly (in Allurus quite certainly) in front of the sperm-duct pores. Dr. Rosa has rebuked me for laying much stress upon the fact that the male pores of Moniligaster are so far forward as the boundary line of Segments x/xi, a position which of course recalls the very anterior position of the corresponding apertures in the generality of the "Limicolæ." It is true that the difference between an opening upon the 10th and 11th segments and one upon the 12th segment is not a very great one, but the difference, such as it is, is in the direction of the lower Oligochæta, and not in the reverse direction.

So much, then, for Moniligaster. The only point in which it differs in an important way from the aquatic forms is in the relatively small size of the ova. The Annelid which forms the subject of the present communication is the only known example of an Annelid with marked affinities to the terrestrial Oligochæta which has that hitherto distinctive character of the lower Oligochæta—large ova filled with yolk.

It resembles the aquatic Oligochæta in the following points:

1. Clitellum consisting of a single layer of cells.

2. Ova very large and full of yolk, few in number, and occupying several segments.

3. Atrium lined by a single layer of epithelium, and covered by masses of pear-shaped cells; sperm-ducts open into it.

4. Longitudinal muscular layer of body-wall consists of a single row of plate-shaped fibres.

The above resemblances are in structures which are, with the sole exception of Moniligaster, confined to the aquatic Oligochæta. Besides these, the genus Alluroides departs from the usual structure of the terrestrial Oligochæta in a few other points, viz.:

1. There is no gizzard, no calciferous glands, and no typhlosole.
2. The nephridia are deficient in the anterior segments.
3. There is no subnervian vessel.

These points do not absolutely distinguish the terrestrial from the aquatic Oligochæta, but they occur in a few of the former while characteristic of the latter. For example, there is no gizzard in certain species of Microscolex; Pontodrilus has no calciferous glands, &c.

The points in which the present genus resembles the terrestrial Oligochæta are by no means numerous. They are as follows:

1. The segments occupied by the clitellum.
2. The position of the male pores, and the fact that the sperm-duct traverses several segments on its way to the external pore.
3. The situation of the ovaries in Segment XIII.

In addition to these, there are some points in which Alluroides agrees with earthworms to differ from the majority of the lower Oligochæta. The sperm masses in Alluroides are confined to the 10th and to the 11th segments; it is the rule among the lower forms for the sperm-sacs to extend much further back. The testes being limited to the 10th segment is rather unusual among earthworms. When there are but a single pair of these gonads they are, as a rule, in the following segment. Among the Lumbriculidæ the testes are in the 9th segment, or, as in Rhynchelmis—and possibly in other genera,—in the 9th and 10th. However, in Phreoryctes the testes are in Segments X and XI, but here the sperm-ducts open on to the exterior in the following segments. The same is the case with the nearly allied Pelodrilus.[1]

[1] "Anatomical Description of Two New Genera of Aquatic Oligochæta," 'Trans. Roy. Soc. Ed.,' 1890.

While we may, as it appears to me, term Moniligaster an earthworm with numerous points of affinity to the "water-worms," it is better to speak of Alluroides as a "water-worm" with affinities to the terrestrial worms. If an exchange could be effected between these two genera of various characters, we should get as a result either an obviously terrestrial genus or an equally obviously "Limicoline" genus. Thus Alluroides would be undoubtedly referable to the terrestrial section of the Oligochæta if it possessed the body-wall and the ova of Moniligaster; on the other hand, Moniligaster would be an undoubted "waterworm" if we could transfer to it the body-wall and the ova of Alluroides.

It is therefore, in my opinion, useless to attempt any comparison with any particular family of terrestrial Oligochæta; it is rather with some family of the aquatic Oligochæta that Alluroides should be compared; be it noticed, however, that, judged by external characters only, Alluroides would probably be referred to the immediate neighbourhood of Allurus.

The family of "waterworms" with which Alluroides has the closest affinities is that of the Lumbriculidæ. It agrees with that family in the following characters:

(1) Setæ paired and S-shaped.

(2) Atrium with thick peritoneal investment.[1]

(3) The great depth of the single layer of longitudinal muscular fibres.

These two characters are found together in the Lumbriculidæ alone among the aquatic Oligochæta; in other respects, however, there are not any striking resemblances between the genus Alluroides and the Lumbriculidæ.

Two of the most characteristic features of this family are wanting in Alluroides; these are (1) the absence (?) of the vascular contractile cæca, and (2) the absence of a second pair

[1] I have shown that in Moniligaster the cells enveloping the atrium are prolonged through the muscular layer and epithelium to open into its lumen; Vejdovsky's figure ('Zeitsch. wiss. Zool.,' Bd. xxvii, pl. xxiv, fig. 3) seems to show that this is also the case with Rhynchelmis.

of sperm-ducts. As to the latter point, I have discovered that in Sutroa the second pair of sperm-ducts are much thinner than the first pair, and that coincidently with commencing disappearance (?) of one of the two pairs of sperm-ducts the testes belonging to the vanishing pair are absent.[1] In my genus Phreodrilus[2] there is a cæcum of the sperm-duct, which is possibly a still further reduced condition of a second pair of sperm-ducts. Among the higher Oligochæta the absence of one pair of testes and of the corresponding sperm-duct is not a matter upon which great weight is usually laid. In any case it appears to me that Alluroides shows no marked affinities to any other family of worms.

Alluroides, gen. nov.

Setæ simple, S-shaped, arranged in pairs; clitellum occupying Segments XIII—XVI, consisting of a single layer only of cells; alimentary canal without a gizzard or any appended glands; some of anterior septa thickened; testes, one pair in X; sperm-ducts open on to exterior on XIII through a moderately long atrium, which has much the same structure as in the genus Moniligaster; above the apertures of the atria is a process of the body-wall (a penis?); ovaries in XI; ripe ova of large size, and filled with yolk, occupy five or six segments of the body; oviducts open on to Segment XIV; spermatothecæ, one pair, without diverticula, in VIII.

The genus contains one species, Alluroides Pordagei, of which I shall not attempt a definition.

1. Gordiodrilus zanzibaricus, n. sp.

A large number of specimens of this species were collected from damp mud at the edge of a pool. They are, when preserved, an inch or so in length. Their colour during life was red.

[1] "A Contribution to the Anatomy of Sutroa," 'Trans. Roy. Soc. Ed.,' vol. xxxvii, p. 195.

[2] "Anatomical Description of Two New Genera of Aquatic Oligochæta," 'Trans. Roy. Soc. Ed.,' vol. xxxvi.

The setæ are strictly paired, and are not in any way ornamented. The pairs are equidistant, and are all of them decidedly ventral in position. The only modification of the setæ occurred on the 17th and 18th segments. On both of these segments only one ventral seta was present on each side; the remaining seta appeared to be the outermost of each pair.

The atrial pores are two pairs, which open on both 17th and 18th segments. Each pore is situated in a groove with raised and somewhat folded margins, which connects the two pores of each side.

The oviducal pores lie a little to the outside of the outermost seta of each ventral pair.

The spermatothecal pores occupy a corresponding position between Segments VII/VIII, VIII/IX.

The clitellum occupies Segments XIV—XVIII, and is complete except over the area lying between the atrial pores.

The nephridiopores lie in front of the inner seta of the outer pair.

The alimentary canal shows the structure which is characteristic of this genus.

In Segment IX is the median ventral calciferous gland, which to describe would be merely to recapitulate my description of other species. From the 9th segment the walls of the œsophagus are highly vascular; the intestine begins in the 13th segment; the intestine is not at first so regularly constricted in successive segments as it is posteriorly, and appears to be of a rather wider calibre. The ciliation of the œsophagus commences just in front of the opening of the calciferous pouch.

The first distinct septum separates IV/V; this septum is thin, but the four following are thickened; the next three septa, though thinner than those which precede them, are thicker than those which follow.

As in other species, there are masses of unicellular glands in the neighbourhood of the pharynx, which have been termed by myself and others "septal glands," on the view that they

correspond to the septal glands in certain genera of aquatic Oligochæta. These glands extend back as far as the 7th segment.

The nephridia are paired structures. The first pair lie in the 5th segment; they are not absent in any of the genital segments; but in the 11th, 12th, and 14th segments the nephridia are more or less rudimentary. That they are present can be made out without any difficulty, for the large vesicular cells which clothe the nephridia from the 9th segment onwards can be readily seen.

The degeneration of the nephridia in these segments must, as it appears to me, be correlated with the development of the genital ducts, or rather their funnels; so complete is this degeneration in the case of the nephridia of Segment XIV that nothing is left but a mass of vesicular cells to tell of the former existence of a pair of nephridia in this segment.

As to the reproductive organs, the testes lie in Segments X and XI, in which are also to be found the funnels of the sperm-ducts; there is nothing unusual in either their structure or their position. The same segments, with the addition of the 12th, contain the sperm-sacs. The sperm-ducts and atria are precisely like those of the West African Gordiodrilus elegans, and call, therefore, for no particular remark. The ovaries are in Segment XIII, and there is nothing remarkable about them or their ducts. There are however, and I have not yet observed this in the genus, egg-sacs in Segment XIV. The spermatotheca are in Segments VIII and IX.

§ Calciferous Glands in the Eudrilidæ.

I have studied with care the calciferous glands in two of the species described in the present paper, viz. Eudriloides Finni and Stuhlmannia variabilis. These two species and another which I have lately described in a paper communicated to the Zoological Society, and named Eudriloides durbanensis, show a peculiar form of these glands which present various points of interest. I find also that Eudri-

loides brunneus has glands of a similar character, but I have not studied them in detail. Michaelsen has not mentioned the existence of these glands at all in the two genera referred to. In fact, he distinctly states them to be absent in the following genera:—Eudriloides, Notykus, Stuhlmannia, Megachæta, and Metadrilus. It is not the case that calciferous glands are absent from at any rate two of the genera mentioned in the above list. But the glands are so little like the usual form of these glands in the Eudrilidæ that it is not at all surprising that their existence has been overlooked.

In Eudrilus and in other genera there are a pair of calciferous glands in the 13th segment or thereabouts, which recall in every particular the calciferous glands of other earthworms. In addition to these there are in Eudrilus, Polytoreutus, Heliodrilus, and Hyperiodrilus unpaired median pouches which agree with the calciferous glands in structure, and are clearly to be referred to the same category. The only ways in which these glands differ from calciferous glands are—(1) their unpaired character—which I am not able to regard as of importance, and (2) the excessive complication of the folded interior of the organ, which is so developed in some forms that the lumen becomes partially intra-cellular. Of these "Chylus-Taschen," as Michaelsen terms them, there are never more than three. In longitudinal and transverse sections of Stuhlmannia, Segments VI—XII are largely occupied by whitish masses on either side of the intestine. These have a paired arrangement, there being a pair to each segment. The shape of these masses is more or less irregular. They are roughly oval with indented margin, as shown in fig. 12; they have in certain regions the form of a coiled tube, the individual coils being closely pressed together. The diameter of each gland varies at different points. The white colour of the glands appears to be due to the presence of innumerable rounded granules which make up the tissue. These granules suggest the yolk spherules of ova. Lying among them are a, comparatively speaking, limited number of small darkly stain-

ing bodies which I take to be nuclei. There is, however, no trace of cell limitations corresponding to the nuclei. The whole gland is covered with a darkly staining but thin sheath. Through the middle of the gland runs a stout blood-vessel, which I found to be nearly everywhere filled with coagulated blood. Its track through the gland was therefore not difficult to follow. The blood-vessel runs through the gland from end to end, but gives off very few branches; it is, however, of such great width as compared with the gland that any branching seems to be unnecessary for the adequate blood-supply of the surrounding tissue. The vessel belonging to each gland could be traced in three directions. Anteriorly it leaves the gland, and traversing the septum becomes the blood-vessel of the corresponding gland of the segment in front. Posteriorly the same thing happens. The successive glands of one side of the body are therefore, as it were, strung upon a continuous lateral vessel. In the middle of each gland a large branch arises from this which communicates with the plexus round the œsophagus. In the case of the last pair of glands, those belonging to the 12th segment, I observed two such branches communicating with the peri-œsophageal blood-plexus of which one was distinctly smaller than the other. Nearly the whole of the gland is made up of the peculiar tissue described and illustrated in figs. 12—15. In places where the gland was very slender in dimensions, this tissue has taken on a decided resemblance to columnar epithelium, faint lines of demarcation between the cells being apparent. Here the appearance presented is that of a tubular gland, but the lumen of the gland is filled with blood. Although these structures are solid, excepting for the blood-vessel which occupies so large a portion of their interior, they are not without communication with the gut. Transverse sections show the nature of their connection with the œsophagus better than longitudinal sections. A transverse section is illustrated in fig. 12. On the ventral surface of the œsophagus a pair of moderately long cellular tubes arise close together from the lining epithelium of the alimentary tract. These diverge, and each follows the

course of the blood-vessel destined for the supply of the gland. It terminates abruptly in the calciferous gland. I am not at all certain that these tubes really possess a lumen; it is at least very inconspicuous, and also the duct is not always so long as that represented in the figure quoted. The aperture into the gut of a second gland is shown in fig. 11. Here it will be seen the duct of the gland is excessively short, and it appears to become solid a very short distance from the point whence it arises from the gut.

Concerning the nature of the peculiar tissue which makes up the greater part of the calciferous gland it is very difficult to speak positively. In several preparations from specimens which had been preserved with Perenyi's solution, the layer of peritoneum surrounding the œsophagus appeared to pass without a break into the tissue of the gland. The appearance of this tissue is, indeed, more suggestive of peritoneal cells than of epithelial cells derived from the intestine. On the other hand, sections of a worm that had been killed and preserved in gradually increasing strengths of alcohol did not show any such gradual passage as has been indicated, for in these sections the peritoneum clothing the intestine was coloured of a greenish tint, and there was a sharp demarcation between this tissue and that forming the bulk of the calciferous glands. Notwithstanding this fact, the tissue in question has more likeness to peritoneal than to any other tissue in the worm's body. The only possible alternative, as it appears to me, is to assume that the cells have retained their embryonic state. In the embryo (not of this species, which is unknown, but of others) the cells of the mesenteron are charged with yolk spherules exactly like those in the gland tissue of the calciferous glands of the adult Stuhlmannia. The structure of the glands in this species is not very widely different from what I have described in Notykus (?) durbanensis in a paper recently published in the 'Zoological Society's Proceedings' (1892). It appeared to me, however, that the lumen of the glands in that worm were rather more developed than in Stuhlmannia. The lumen was quite obvious, though of little extent. The

glands, too, were of a more regular form, and showed no modification of the peculiar cells of the gland such as occurs in places in the gland of Stuhlmannia. I have now to record the structure of the corresponding glands of Eudriloides Finni. In this worm the glands are rather different in the details of their histology. There are pairs, but there is not always an absolute separation between the glands of adjacent segments. In a few cases I have found that there is a communication from segment to segment. The tissue composing the glands is for the most part exactly as in Stuhlmannia. The glands, however, are more irregular in form and the blood-vessel is much more coiled; where it (the blood-vessel) leaves the gland the tissue surrounding it is reduced to a comparatively thin layer. As the vessel with the surrounding tissue is much coiled, the appearances of a transverse section through a portion of the gland are much as is shown in fig. 15. This section presents a most curious resemblance to a section through the thyroid gland. It has every appearance of tubes of columnar epithelium surrounding a lumen which is filled with a homogeneous secretion; this "secretion" is nothing but blood. I have, of course, traced the supposed blood-vessels into connection with the vascular system. The modification of the tissue of the gland is not gradual; here and there it suddenly passes into the tissue illustrated at *c* in fig. 15. The tissue in question stains much more darkly than the rest of the gland, the granules in the cells which compose it are disposed in a radiate fashion, and the cells have acquired a columnar appearance, of which indications are observable in Stuhlmannia, as I have already pointed out. The specialisation of the cells is much more marked in the present species. It will be clear, at least from the figures which illustrate the foregoing description, that the glands which I call "calciferous" are not only different in the three genera referred to from those of other Eudrilids, but are also different—very different—from the corresponding glands of nearly all other earthworms. The only genus which at all approaches these Eudrilidæ in the structure of its calciferous glands is my genus Gordiodrilus. In all the species

of this genus there is a single calciferous gland or rarely a pair of these glands in the 9th segment ventral in position. The genus Gordiodrilus is mainly an African genus; it has been found in West Africa, and I describe in the present paper a species from Zanzibar. Gordiodrilus has no marked affinities to the Eudrilidæ, and for the present I place it in that unsatisfactory family the Cryptodrilidæ. The only point of resemblance to the Eudrilidæ is in the median and unpaired calciferous gland. This gland is a diverticulum of the œsophagus, which is surrounded by a mass of tissue exactly like that which makes up the greater part of the glands in Stuhlmannia and Eudriloides. The œsophageal diverticulum, however, passes from end to end of the gland, and expands at its blind extremity into a network of fine tubes having an intra-cellular lumen and bearing the strongest possible likeness to nephridial tubes. This genus is noteworthy from the present point of view as furnishing an intermediate condition between the calciferous glands of the more typical earthworms and those of the genera Stuhlmannia, Notykus, and Eudriloides. The lumen connected with the œsophagus is reduced in extent and is not folded, while at the same time the peritoneal covering is greatly increased in importance. The next stage is furnished by Notykus. Stuhlmannia seems to me to have a still more reduced œsophageal diverticulum. Finally, in Eudriloides I could not detect any diverticulum at all. In this species the walls of the œsophagus were much folded, so that a short diverticulum, if it exists, would be less conspicuous than in Stuhlmannia. As the extent of the epithelial diverticulum of the œsophagus is lessened there is a corresponding increase in the amount and also in the specialisation of the peritoneum-like tissue which surrounds it. Already in Stuhlmannia there is a commencing conversion of some of these cells into a definite layer bordering the blood-vessels in certain regions. In Eudriloides the amount of this specialised tissue is increased and the specialisation has gone further. It appears to me that this remarkable change in the histological characters of glands, which I cannot but consider to be the homologues

of the calciferous glands, must indicate a change in function.

In the present state of our knowledge, we can do no more than guess what this change of function can be. We are helped, however, by certain facts in the histology of the glands, and by the analogies offered in other animals. The structural change undergone by the calciferous glands is a reduction of the lumen, and presumably, therefore, a rapidly decreasing amount of secretion furnished to the œsophagus. I have never, it should be mentioned, seen the least trace of any calcareous particles in the calciferous glands in either Gordiodrilus, Stuhlmannia, Notykus, or Eudriloides. As the secreting tissues diminish, the tissues surrounding the glands increase in amount and in specialisation. They are supplied with blood from a large vessel which is dilated within the gland, and by its devious course must prolong the time that the blood is submitted to the action of the surrounding cells. The function of these glands must, I believe, have some relation to the blood. I regard them as analogous to the spleen of the Vertebrata; and in relation to this matter it may be pointed out that it has been stated that the spleen is originally formed as a diverticulum of the gut, thus indicating a conversion from a gland appended to the alimentary tract, and probably performing the function of a digestive gland to a "gland" concerned in some way with the blood. The instances described in the present paper are remarkably analogous. A series of glands undoubtedly related to the function of digestion are metamorphosed into glands which also appear to have some relation to the vascular system. In the family Enchytræidæ there is something of the same kind. The genera Buchholzia and Henlea are furnished with glandular appendages to the œsophagus, which can hardly be different in their nature from the calciferous glands of earthworms; from these glands (in most cases) the dorsal vessel arises. In the genus Mesenchytræus there are no such glands, but the dorsal vessel at its origin from the periœsophageal plexus (or sinus) contains a cellular rod which has been called the "cardiac

body." I agree with Michaelsen in considering this structure as the reduced equivalent of the œsophageal diverticulum, which, if it has any function at all, must perform some office in relation to the blood. In this connection, also, I may refer to my own description of an analogous organ in the fresh-water Oligochæte Phreodrilus. In that worm there are a pair of perienteric blood-vessels of larger size than the rest which contain in their interior masses of cells. These, too, may be the last stage in the conversion of an alimentary gland into a "blood gland." Of a different nature are probably the vascular tufts which arise from the dorsal vessel in many Lumbriculidæ; though here, too, the error of Grube in terming these vascular cæca diverticula of the intestine is not unsuggestive. Finally there are the "blood glands" of Perichæta, which I have described in a recent volume of this Journal. These are hardly referable to œsophageal diverticula which have lost their connection with the gut. Their existence is interesting as showing the possibility that in the Annelids we have a group of glands very suggestive of the spleen, supra-renal bodies, and perhaps some other of the "ductless glands" of the Vertebrata which are not all traceable to a common origin. Mr. Weldon has shown how the supra-renal body derived from the renal epithelium has lost its renal function and become converted to the interests of the vascular system. His description and figures of blood-clots lying in the lumen of the tubes is of particular interest to me in connection with the structures illustrated in fig. 15 of the present paper; but in making this comparison, it would be necessary to assume that the cells which I have regarded as peritoneal were in reality metamorphosed epithelium of the calciferous glands.

The only other Eudrilid in which calciferous glands, after the pattern of those described in the present paper in Stuhlmannia and Eudriloides, seems to be Megachæta tenuis. Michaelsen writes as follows about the matter:—"In den folgenden Segmenten erkennt man je ein Paar eigenartiger, Fettkörper-ähnliche Organe, die zu Seiten des Darmes liegen.

Die Zellen, aus denen diese Körper bestehen, sind grob granulirt und erhalten durch Einlagerung zahlreicher, schwarzer Korner ein Chloragogenzellen-artiger Aussehen. Ein starkes Blutgefäss geht mitten hindurch. Ich glaube erkannt zu haben, dass diese Körper mit den Segmentalorganen zusammenhangen, deren in je einem Segment ein Paar vorhanden ist. Es musste unentschieden bleiden, ob sie durch die ganze Lan ge des Körpers oder nur am Vorderkörper ausgebildet sind. Soweit ich das Tier untersuchte, bis zum 20. Segment, sind sie vorhanden." It seems to be possible that the structures which Michaelsen here describes (without any figures) are the same as the organs regarded by myself as the metamorphosed equivalents of the calciferous glands of other Eudrilids. The account of the minute anatomy which Michaelsen gives, though not very full, agrees so far as it goes with the organs in question. They have a kind of resemblance to a fat body, and the cells of which they are composed are distinctly "grob granulirt," but they do not, so far as my own observations go, contain any black pigment. Another difficulty, and the most serious one in the way of comparing the glands of Megachæta with those of Stuhlmannia, &c., is the fact that in the former genus they extend back as far as the 20th segment. This is too far, one would be inclined to suppose, for glands to extend which are homologous with calciferous glands, connected as they are in all earthworms with the œsophagus. The close proximity of the nephridia to the glands might easily give the impression that the two series of organs were connected. The fact that they are traversed by a strong blood-vessel is another point of resemblance to the calciferous gland of Stuhlmannia, &c.

§ Note on the Substitution of Organs as Illustrated by the Spermatothecæ in the Eudrilidæ.

I do not think that attention has been directed to the excellent instance which the spermatothecæ of the Eudrilidæ afford of the substitution of one organ for another (physio-

logically identical, but morphologicallly different). The principal feature of interest in the anatomy of the Eudrilidæ is the presence of cœlomic sacs which do duty as spermatothecæ. I have called these sacs consistently "spermatothecal sacs" to mark their difference in structure from, but their similarity in function to, the spermatothecæ of other Oligochæta. Michaelsen, it is true, has denied to the spermatothecal sac of the Eudrilidæ the function of storing sperm. They have, however, been proved to contain sperm in Nemertodrilus, Eudrilus, and Polytoreutus. That these sacs are not homologous with the spermatothecæ of other Oligochæta is shown by their development. I have pointed out that in Libyodrilus the sac is formed at the expense of the septa, and Rosa has arrived at the same conclusion by a consideration of the histological structure of the sac in Paradrilus. There is, however, at least one genus in which the spermatotheca appears to be of the type general in the Oligochæta. In Heliodrilus there is a single long and narrow sac which opens externally on to the 11th segment, and reaches back to the 13th. At the extreme end the spermatotheca is enclosed by a cœlomic sac continuous with the ovarian sac, &c. I have no facts of development to offer in support of my belief that the spermatotheca in this Annelid is comparable in origin to that of other earthworms; I rely upon its structure and relations. The sac in question is lined by a columnar epithelium, quite different in appearance from the cells which line the sac in which it lies, but quite like the cells which are found in the spermatothecæ of other worms, in which these organs are epidermic invaginations. This is, I hope, plainly shown in the figures illustrating my account of the anatomy of Heliodrilus. The next stage is seen in Hyperiodrilus. Here we have the true spermatotheca reduced to very small dimensions, and the sac involving it is greatly increased in size. In Paradrilus it is possible, whether it actually occurs or not, for sperm to reach the interior of the large cœlomic sac; for this sac communicates directly with the exterior by a short tube which seems to be an invagination of the epidermis, and

appears to be the equivalent of a part of the spermatotheca of Hyperiodrilus. The genus Eudriloides which I have dealt with in the present paper supplies the next stage. Here we have a cup-shaped layer of cells which, though they have lost their connection with the epidermis, are very possibly to be regarded as a derivative of it. They do not, however, line the cœlomic pouch, but have been, as it were, thrust aside by the growth of the cells lining the sac, which cells have forced their way to the exterior. Here, therefore, the original spermatotheca is entirely relieved of all share in the organ devoted to the storage of the sperm. Finally, Libyodrilus and perhaps Polytoreutus have no trace left of the original epidermic invagination except possibly at the very pore. I have shown in Libyodrilus that the sac which is formed out of the tissues of the septa, burrows its way into the thickness of the body-walls; it is quite likely that it actually reaches and perforates the epidermis by its own unaided efforts. The spermatotheca, therefore, of Heliodrilus gradually yields up its place to the sac developed out of the mesoblastic tissues, which grow as it diminishes, and finally entirely replace it. This instance is quite analogous, for example, to the replacement of the notochord by the vertebral column.

§ Classification of the Eudrilidæ.

This family comprises now so large a number of forms that it may be desirable to subdivide it. A subdivision has been attempted by Michaelsen (loc. cit.); but it seems to me that a further acquaintance with the structure of the various genera of the family does not tend to confirm the justice of dividing the family, as Michaelsen does, into two sub-families, Eudrilini and Teleudrilini. The diagnosis which Michaelsen gives of the Teleudrilini is as follows:

"Die Teleudrilinen sind meganephridische, mit 4 Borstenpaar-Reihen ausgestattete Terricolen, die eine einzige ventral-mediane männliche Geschlechtsöffnung auf oder am 17 Segment und eine einzige ventral-mediane Samentaschenöffnung hinter der Intersegmentalfurche 10/11 besitzen."

The two sub-families are, in fact, distinguished by the median or paired character of the generative apertures alone. In the absence of any other characters it appears to me that the paired or unpaired character of the apertures in question is by no means a difference of first-rate importance. Even if we follow Michaelsen in separating as a distinct genus the Cryptodrilid Fletcherodrilus on account of its median series of spermatothecæ, no one would in all probability consider that genus to be worthy of being placed in a separate sub-family, nor, indeed, does Michaelsen propose anything of the kind. The median spermatotheca of Sutroa does not disguise its likeness to other Lumbriculidæ. And in general there are so many instances in the group of the Oligochæta of structures which are paired in one genus and unpaired in another, that a division so pronounced as that which Michaelsen proposes does not commend itself to me.

There are two characters which seem to me to afford a more reliable means of subdividing this family into two sub-families, should such a step be regarded as necessary; as they both relate to structures which are highly characteristic of the genera in which they occur, more weight is to be attached to them. The genus Eudrilus, when it was the only Eudrilid known, was shown by myself to differ from all other earthworms by the possession of ventral median unpaired pouches, which Michaelsen termed "Chylustaschen." The fact that these structures are unpaired is not alone a fact that is greatly to be valued, though it may be pointed out that Gordiodrilus is at present the only other genus (not a Eudrilid) in which these so generally present, and with these exceptions paired, structures are to be found. The most remarkable fact about these unpaired pouches is that they coexist with one pair of paired pouches not lying in the same segment as any one of them; this is more remarkable than if all the calciferous glands were paired or unpaired, as the case might be. Another (at that time quite unique) character of Eudrilus is the existence in the epidermis, or rather just below it, of numerous integumental bodies, which Dr. Horst and I myself have compared to the Pacinian

bodies of the Vertebrata; their appearance, at least, is very like that of the structures mentioned. These same characters are found in a few other genera of Eudrilidæ; they occur in Teleudrilus, in Hyperiodrilus, and Heliodrilus (which two latter Michaelsen unites into a single genus), and finally in Polytoreutus. I am in a position to state that the integumental sense-organs—if I am justified in applying the term "sense-organs" to them—are absent in the following genera:—Eudriloides, Heliodrilus, Pareudrilus, Nemertodrilus, and Stuhlmannia. In none of these genera are there calciferous glands at all like those of the genera mentioned in the first list. Libyodrilus, Pareudrilus, Alvania, and Nemertodrilus have no calciferous glands at all—not a trace of them. In the remaining forms the calciferous glands have undergone the peculiar modification that has been described on a previous page. I think that these two characters serve to distinguish two groups of Eudrilidæ better than the paired or unpaired generative apertures. I would furthermore remark that the condition of the glands, which I believe to be the representatives of the calciferous glands of other Eudrilidæ—in the genus Eudriloides, for example—is not in accord with the low position among the "Teleudrilini" to which Michaelsen assigns it.

These genera are the only ones in which both the points used for the subdivision of the family are known; in some others the presence or absence of calciferous glands has been noted. Thus both Michaelsen and Rosa have shown the existence of a single pair of calciferous glands in the 12th segment in the genus Paradrilus. Preussia is said to have a pair of these glands in the 12th segment; but Michaelsen is doubtful about their nature, and has stated that they contained no calcareous particles. Platydrilus, Megachæta, and Metadrilus have, according to Michaelsen, no calciferous glands, and the remaining genera are not described in this respect. It will be noticed that in the two groups into which I have provisionally divided the family there is yet another character which divided them, and which may possibly be of

value. In Eudrilus and the genera which are placed with it, the sperm-ducts are dilated into a round or oval sac before they open into the funnel. Michaelsen terms these dilatations "Eiweisskapseln." These oval dilatations are absent in all the genera which I have placed in the second group. Paradrilus has them, and, as it also has at least one pair of calciferous glands, may perhaps be referred to the first group. Such dilatations appear to be absent in the genera Platydrilus, Megachæta, Metadrilus, and Notykus. These genera have, as has already been pointed out, no calciferous glands; it remains to be shown whether the integumental sense bodies are absent. Provisionally, therefore, I group the Eudrilidæ[1] into—

Sub-family 1. Eudrilinæ.—Calciferous glands present. Integumental sense organs generally present. Funnels of sperm-ducts dilated proximally.

Sub-family 2. Pareudrilinæ.—Calciferous glands absent or greatly modified. No integumental sense-organs.[2] No dilatation of sperm-ducts.

[1] It is very possible that the structure of the nephridia will prove to separate these two groups. I have to some extent dealt above with the excretory organs of a few types belonging to the sub-family Pareudrilinæ; in these there is either a well-developed integumental plexus of tubules or traces of such. On the other hand, nothing of this kind occurs in any of the Eudrilinæ.

[2] Except in Eudriloides (occasionally).

EXPLANATION OF PLATES 16 & 17,

Illustrating Mr. Frank E. Beddard's paper, "A Contribution to our Knowledge of the Oligochæta of Tropical Eastern Africa."

FIG. 1.—Transverse section through atrium of Eudriloides Cotterilli. *v. d.* Vas deferens, alongside of which runs a blood-vessel.

FIG. 2.—Transverse section through atrium of Eudriloides brunneus, just at the point where the two atria join. *v. d.* Vas deferens. *gl.* Glandular cells containing abundant secretion.

FIG. 3.—Transverse section through atrium of Polytoreutus violaceus. *bl.* Blood-vessel. *m.* Special thickenings of muscular coat.

FIG. 4.—Alluroides Pordagei; lateral view of anterior segments. *sp.* Spermatothecal pore. ♂. Penis. ♀. Oviducal pore. The clitellum is indicated by the absence of furrows dividing its segments.

FIG. 5.—Alluroides Pordagei; longitudinal section through atrium and adjacent structures. The segments are numbered. *Cl.* Anterior, *Cl'.* Posterior end of clitellum. ♂. Male pore. *p.* Penis. *o.* Ovary. *At.* Atrium. *od.* Oviduct. *ov.* A ripe ovum.

FIG. 6.—Polytoreutus Finni. Spermatothecal sacs and atria. *s.* Spermatothecal sacs. ♀. Oviducal pores. ♂. Terminal muscular sac in which atria (*At.*) open. *sp.* Terminal sac through which spermatothecal sacs open.

FIG. 7.—Polytoreutus violaceus. Spermatothecal sacs and atria. Lettering as in Fig. 6.

FIG. 8.—Polytoreutus kilindinensis. Spermatothecal sacs and atria. *v. d.* Sperm-duct. *v. d. f.* Its funnel, opening into interior of *s. s.*, sperm-sac.

FIG. 9.—Reproductive organs of Pareudrilus stagnalis, displayed by dissection and in sitû. *œs.* Œsophagus. *E. s.* Sac containing ovary, and connected with spermatothecal sac. *Sp.* Orifice of latter on to exterior. *Ro.* Egg-sac. ♀. Oviducal pore. ♂. Terminal sac of *At.*, atrium. *p. s.* Sac containing penial setæ.

FIG. 10.—Genital segments of Eudriloides brunneus, from beneath. ♀. Spermatothecal pore. ♂. Male pore. *Cl.*, *Cl'.* Anterior and posterior boundaries of clitellum.

FIG. 11.—Longitudinal section through a few segments of Stuhlmannia variabilis in œsophageal region. *Œs.* Œsophagus. *Ca.* Calciferous glands. *D. v.* Dorsal vessel. *S.* Septum. *Ep.* Epidermis. *m.* Muscular layers of body-wall.

FIG. 12.—Transverse section through œsophagus and one of calciferous glands of the same. *œs.* Œsophagus. *d.* Duct of gland opening into it. *a.* Extremity of gland where nuclei are arranged in irregular portions on each side of a blood-vessel.

FIG. 13.—A portion of a calciferous gland of same, more highly magnified to show the nuclei (*n.*), the boundaries of the cells (*l.*), and the secreted granules (*s.*).

FIG. 14.—Extremity of calciferous gland, lettered *a* in Fig. 12.

FIG. 15.—Section through a calciferous gland of Eudriloides Cotterilli. *c.* Modified cells of gland closely investing the blood-vessels.

FIG. 16.—Section through end of spermatothecal sac of Eudriloides Cotterilli. *Ep.* Epidermis. *Pl.* Plug of cells occluding lumen of sac. *m.* Mesoblastic cells lining it. *E.* Layer of epiblastic cells, apparently invaginated to form wall of sac.

FIG. 17.—Genital segments of Polytoreutus Finni. ♀. Spermatothecal pore. ♂. Male pore.

FIG. 18.—Terminal male apparatus of Eudriloides Cotterilli. *At.* Atria. ♂. Male pore. *s.* Penial seta. *a—e.* Muscles referred to in text.

FIG. 19.—Spermatothecal sac of the same. *gl.* Its glandular appendices.

FIG. 20.—End of penial seta of the same.

FIG. 21.—Terminal male apparatus of Eudriloides brunneus. *v. d.* Sperm-duct. Other letters as in Fig. 18.

FIG. 22.—Spermatothecal sac of the same. *x.* End of sac lying in front of external pore. *gl.* Glandular appendices.

FIG. 23.—Transverse section through part of spermatothecal sac, lettered *x* in last figure.

A Further Contribution to the Anatomy of Limnocnida tanganyicæ.

By

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With Plates 18 and 19.

The present paper is the result of a more minute examination of the same material on which my preliminary account of Limnocnida was based. Having already treated in my previous paper of the more obvious characters of the Medusa, I have endeavoured to avoid needless repetition in the present. The material had been caught and fixed in osmic acid by Mr. A. Swann on the shores of Lake Tanganyika itself, and reached me in a good state of preservation in strong alcohol, as already mentioned in the preliminary notice.

The present work was carried out in the new Morphological Laboratory at Oxford during Lent term, 1893; and I have to express my sincere thanks to the President and Fellows of Magdalen College for enabling me to pursue my studies in Oxford, and also to Professor Ray Lankester for all the facilities which he afforded me while working in his laboratory.

The following account of Limnocnida is divided into three sections. The first is devoted to the description of certain parts of the anatomy of the Medusa, and the arrangement adopted by O. and R. Hertwig in their 'Organismus der Medusen' has been followed in the main. The second and third parts deal with the systematic position of Limnocnida and the origin of fresh-water Medusæ respectively. At the

end of the first part is a full description of the process of reproduction by budding in Limnocnida, which was only briefly referred to in my preliminary account.

I. Anatomy.—a. The Ectoderm.

The general limiting epithelium of the body does not call for particular remark. It consists of a single layer of polygonal cells, which vary in height at different parts of the surface. On the more exposed surface of the exumbrella they are more or less flattened, while on the subumbrella and velum they are cubical or even slightly columnar in places. The nucleus is roundish, and usually situated in the middle of the basal half of the cell.

Thread-cells were only observed on the tentacles, arranged in groups or batteries, on the margin of the umbrella, thickly packed in a continuous ring, and on the manubrium, distributed along the edge. The exumbrellar surface seems to be completely destitute of any such groups of thread-cells as occur in the Æginidæ or the Geryonidæ. The thread-cells themselves are very small oval bodies, the major axes of which are about twice as long as the minor axes. A peculiar modification of the ectoderm, analogous to the peronium of the Trachynemidæ and Geryonidæ or to the nettle-ring of Limnocodium, occurs all round the rim of the umbrella, just outside the circular canal. This ring of modified ectoderm extends over the roots of the tentacles, and in it are buried the marginal sense-organs (Pl. 18, figs. 1 and 2). The minute structure is very similar to that of the peronium of other Medusæ, and, like that organ, apparently consists of modified thread-cells. Its function is possibly skeletal as well as defensive.

Muscular System.—Muscle fibres probably exist both on the exumbrella and on the subumbrella, but they could not be demonstrated in the material at hand with any degree of certainty. The muscles of the velum, however, are very conspicuous, both in preparations mounted whole and in transverse sections. The ectoderm of the inner surface of the velum

gives rise to a number of strong circular muscle-bands, which may be seen in transverse sections to project into the mesoglœa. Near the point of attachment of the velum, the muscle-bands are small with a simple semicircular transverse section, but as they approach the free margin of the velum, they become larger and their transverse sections lobulated. From this it appears that the muscle-bands near the free edge of the velum are those which are chiefly concerned in the contraction of the organ.

Nervous System.—No trace of a nervous system could be observed in transverse sections, although special search was made for a nerve-ring in the neighbourhood of the base of the velum.

Sense-Organs.—The sense-organs or marginal bodies are embedded on the velar side of the zone of ectoderm which constitutes the nettle-ring. In all the individuals examined no relation could be demonstrated between the arrangement of the marginal bodies and that of the tentacles, though it is not improbable that some radially symmetrical disposition may occur in younger stages. It would seem that new marginal bodies are continually being developed, as even in the oldest individual examined quite young sense-buds were observed. In my former paper I suggested that the marginal bodies would be shown to be endodermal in origin, from the analogy of the corresponding organs in Limnocodium. It can now be definitely affirmed that the axial part of these organs is also of endodermal origin in Limnocnida. In Pl. 18, figs. 1 and 2, there are figured two sections passing through a young marginal sense-organ (*A*). It will be seen that the mesoglœa (*ms.*), which is present almost everywhere between the ectoderm of the nettle-ring and the endoderm of the circular canal, is broken through just beneath the base of the young sense-organ, and certain endoderm cells project from the endoderm into the young sense-bulb. In fig. 1, *x.* is such an endoderm cell actually wandering from the endoderm to take up its place in the axis of the sense-organ. The direction of movement is indicated by the edges of the perforation in the

mesoglœa being slightly turned up, forming a sort of "burr" on the side of the ectoderm.

The sense-organ consists of an almost spherical sense-bulb and a containing capsule. The sense-bulb is composed of a number of clear, refringent nucleated cells, sometimes arranged in two layers, as in fig. 2, *B*, where several large central cells (four are seen in the figure) are surrounded by numerous flattened cells, but more often the central and sheathing cells are so mixed up that it is impossible to distinguish between them. At the base of the sense-bulb there are generally a few very granular cells, by which the bulb is attached to one wall of the capsule. The capsule is buried in the nettle-ring and lined by an endothelium of very thin pavement-cells.

In the young sense-organ the bulb consists of a number of squarish peripheral cells, all grouped round one or more large axial granular cells (figs. 1 and 2, *A*.). In the young organ there is not so much space between the wall of the capsule and the bulb as in the fully-grown organ. The endodermal axis of the fully-grown organ is completely shut off from the endoderm of the circular canal, from which it has sprung, by a thick plate of mesoglœa.

Generative Organs.—As is the case with the Ocellata, the genital organs are developed from the ectoderm of the manubrium. In sexually mature animals the ectoderm of the proximal two thirds of this organ is very much thickened owing to the prolific growth of the sexual elements in this region. Inside the area occupied by the genital organs the endodermal lining of the œsophagus is modified (figs. 3 and 4, *end.*). It is much thickened, and consists of long cells, the outer ends of which are probably flagellated, though the flagella were not preserved in the material examined. The protoplasm contains numerous granules of foreign matter, and, as in similar cases described by Hertwig (7), "has a plant cell-like appearance." The mesoglœa becomes unusually thin in the region of the sexual organs, though tolerably thick on either side of that region. Thus far, the structure of the manubrium in the region of the genital organs

is the same in both males and females. It is only the ectoderm which is different in the two sexes; but in both, the general type of structure of the germarium is similar.

In both spermarium and ovarium of Medusæ the Hertwigs distinguish three layers, viz. I, a basement layer; II, a layer of germ-cells in various stages of development; and III, a covering epithelium. In Limnocnida, layers I and II are so intermingled that it is hard to draw a hard-and-fast line between them (figs. 3 and 4).

The cells which correspond to layer I lie next the mesoglœa. Their nuclei are relatively large and round. In the male there are usually several layers of cells, all of the same nature. In both sexes these cells may be regarded as the germ mother-cells, and it is from them that the cells of the next layer originate.

Layer II is composed of ova or spermatozoa in various stages of development. On comparing sections taken through the germaria of the two sexes (figs. 3 and 4) the general distinguishing features are strikingly brought out. In the male the germ-cells tend to become as numerous and as small as possible, while in the female all available material is employed in the construction of a few gigantic ova. In the section of a spermarium shown in fig. 4, two stages of development are seen. The innermost cells have large round nuclei, nearly twice as large as the nuclei of the parent cells from which they are derived. These cells eventually give rise to clusters of numerous cells with very small nuclei, which stain more deeply than those of the large cells. At a later period these small cells will probably grow tails and become mature spermatozoa, but among the specimens examined none were found with mature spermatozoa developed.

In the female the cells of the second layer are much larger and fewer in number than in the male. It is composed of two kinds of cells (fig. 3, *ov.* and *st.*), both of which are derived from the first layer. The most conspicuous cells in this middle layer are ova (fig. 3, *ov.*), and attain to a very considerable size. They are by far the largest cells in the body of the Medusa.

Their shape is rounded, and they are often provided with a few processes extending inwards between the other cells towards the cells of the first layer. Their protoplasm is exceedingly granular, and contains one or more large vacuoles. The nucleus is a very large clear spherical body in the centre of the cell, which hardly stains at all, almost all the chromatin being concentrated in the large nucleolus. The other kind of cells differ from the ova in their protoplasm being quite clear and free from granules, and in their not growing to such a large size. From the way in which they are situated with regard to the ova, they would seem to be merely packing or interstitial cells (fig. 3, *st.*).

The third or outer layer is the same in both sexes. It consists of a covering epithelium of more or less cubical cells with round nuclei (figs. 3 and 4, *ect.*). In the female the cells are somewhat more irregular in shape than in the male.

B. The Endoderm.

Epithelium of Gastro-vascular System.—The endodermal lining of the manubrium in the region of the sexual cells has been described above in the section on the reproductive organs. On either side of this region the endoderm cells (fig. 5, *end. m.*) have much the same internal granular structure, but they are not so long. The epithelium covering the dorsal wall of the stomach is represented at *end.* in fig. 5. It consists of granular columnar cells with a clear space towards their free ends. No traces of intracellular digestion were observable in any of the cells of the gastric epithelium. The radial and circular canals are lined with squarish polygonal cells, many of which are vacuolated. The epithelial lining of the circular canal on the side nearest the nettle-ring is thrown into folds (*end.*, fig. 6), the cells of which are sometimes so tightly packed as to obscure the divisions between the folds. In this way a highly peculiar endodermal organ is formed in the circular canal, which may grow to such an extent as to completely fill the lumen of the canal. The cells of this

organ are multinucleate and, in some regions, vacuolated. Moreover, spaces may occur in this hypertrophied mass of cells within which one or more of the cells may be floating. Similar cells (fig. 7) occur in the lumen of the circular canal and in the radial canals. In all, the nucleus is broken up into several pieces, and in many, vacuoles are present.

The function of this extraordinary organ of the circular canal is extremely doubtful. Nor are there any means of settling the matter until living material can be obtained for examination.

The abundant discharge of the cells which are found in the circular and radial canals, would indicate an excretory function by which noxious or useless matter is carried to the exterior. On the other hand, it is possible that the organ is endowed with the power of secreting some digestive ferment which is discharged into the circular canal and is thence conveyed into the shallow gastric cavity by the radial canals; or, again, the katalysis of the free cells themselves may supply a material of economic value to the organism.

The endoderm lamella is situated very close to the sub-umbrellar ectoderm and is composed of a single layer of small cubical cells which increase in size and become vacuolated near the gastric cavity (fig. 6, *end. l.*).

The tentacle axes are hollow and composed of large, clear, thin-walled cells, each with a small nucleus on one side. The cell contents seem to be almost entirely fluid or gelatinous, and hardly any trace of granular protoplasm can be made out. It is probable that the turgidity of these cells may be the cause of the rigidity of the tentacles. The lumen of the tentacle is continuous with that of the circular canal, as seen in the section figured in fig. 6, which passes through the base of one of the radial tentacles.

c. Reproduction by Budding.

In certain of the individuals examined, the external wall of the manubrium was found to be covered with numerous small Medusa buds in various stages of development. The region

which is capable of giving rise to buds forms a zone completely surrounding the manubrium and covering about two thirds of the surface of that organ, leaving a distal zone free from buds, as in Sarsia. Thus the area on which Medusa buds may develop is approximately co-extensive with the germinal area on which the reproductive elements may arise in sexual individuals.

The ectoderm cells of the gemmiferous region of the manubrium are much vacuolated; their nuclei for the most part lie deeply, close to the endoderm, but some have a more superficial position between the vacuoles. Cell boundaries are either altogether absent or could not be demonstrated. The cells of the endoderm of this region are arranged in several layers; in character they are polygonal, very granular, and provided with definite walls. The mesoglœa, which is nowhere very thick, disappears altogether beneath the larger buds. It is thickest in the distal third of the manubrium, in the region which does not give rise to either medusa buds or generative products.

The young bud first makes its appearance as a small local outpushing of the wall of the manubrium. This outpushing (figs. 8 and 8 *a*) affects all the cell layers and is hollow, its cavity being a diverticulum of the gastric cavity of the parent. Thus a part of the digestive epithelium of the parent becomes the endoderm of the young bud, and it is not unlikely that by means of this endoderm the bud may obtain the nutriment for its further growth by the direct absorption of such food matter as may enter its own "stomach" from the gastric cavity of the parent.

The young bud does not remain long in this stage. A change soon appears to come over the ectodermal cells at the apex of the bud. Their protoplasm instead of being vacuolated becomes dense and more granular than before, while the cells themselves become somewhat thicker, and their nuclei take up their position in an even row next the endoderm. These changes foreshadow the next step. The apical ectoderm bodily invaginates into the endoderm (figs. 9 and 9 *a*) at the tip of the

bud to form the "glockenkern" (*gl.*) or forecast[1] of the ectodermic lining of the subumbrella cavity. As the ectodermic invagination sinks deeper into the interior of the bud, its cells acquire definite walls and arrange themselves in a single layer round a central cup-shaped space. The mouth of this space now closes up, and finally the entire "glockenkern" becomes covered over by an overgrowth of ectoderm, and its cells become marked off from the cells of the peripheral ectoderm (figs. 11 and 11 *a*, *gl.*). At this stage the "glockenkern" is a hollow sphere of ectoderm, one cell thick, enclosing a hollow cavity, which, as has been shown above, is really a portion of the exterior which has been enclosed during the growth of the bud. Meanwhile, owing to the invagination of such a comparatively bulky mass of ectoderm, the endoderm thins out so much as to be reduced to a single cup-shaped layer of cells enveloping the central "glockenkern."

A second ingrowth of ectoderm now occurs. The ectoderm cells at the apex of the bud become less vacuolated and undergo changes similar to those which the cells of the "glockenkern" passed through, and grow down as a solid plug of cells into the apex of the "glockenkern." Before this stage is reached the "glockenkern" was more or less spheroidal or egg-shaped, but the effect of the second ingrowth of ectoderm is to push one wall of the "glockenkern" into the other, with the consequent result that the "glockenkern" becomes a two-layered cup surrounding a plug of ectoderm cells. A further result is that the lumen of the "glockenkern"—the future subumbrella cavity —becomes considerably reduced in size and may even, in some cases, disappear altogether (figs. 12 and 12 *a*). In the latter case it always reappears at a subsequent stage. The outer wall of this cup-shaped "glockenkern" will ultimately form the ectoderm of the subumbrella, while the inpushed wall will

[1] I have used this word as the English equivalent of the word "Anlage," which has presented so much difficulty to translators. The use of the terms "rudiment" or "fundament" (Prof. E. L. Mark) is not to be recommended in this sense. For some considerable time past the members of Professor Lankester's "Seminar" at Oxford have been accustomed to use the term "forecast" with the significance of "Anlage."

give rise to the subumbrella side of the velum—the outer side of the velum being formed from the second ingrowth of ectoderm, as will appear in the sequel.

By the next stage the forecasts of most of the important organs of the Medusa can be readily recognised (figs. 13 and 13 *a*). The subumbrella ectoderm (*s. ect.*) and velar ectoderm (*v. ect.*) have become much thinner relatively. The subumbrella cavity (*s. c.*) is very large. The endoderm cells surrounding the "glockenkern" have grown further over that organ, and at certain regions have begun to grow up into the mass of ectodermic cells at the apex of the bud, thus indicating the positions of the future tentacles. At this early stage the forecasts of the tentacles are solid, but in section their endodermal axis (*t. end.*) may be shown to be composed of numerous cells arranged round a central axis. A lumen does not appear until a somewhat later stage. Of the tentacles, four are greatly in advance of the others, but I was not able to make out whether two of these make their appearance before the other two, as is often the case among the Hydrozoa.

Meanwhile a great change takes place in the apical mass of ectoderm. Its constituent cell nuclei, instead of being more or less uniformly diffused throughout the mass, now assume definite positions with regard to the neighbouring organs (fig. 13). The more deeply seated nuclei range themselves in a single tier along the outer side of the "glockenkern," while the others surround the forecasts of the endodermal axes of the tentacles. In the section through a Medusa bud of this stage in fig. 13, a small space may be seen between the ectodermic epithelium of the tentacles and the ectoderm overlying the "glockenkern." The subumbrella cavity at this stage still remains completely closed by a membrane composed of part of the "glockenkern" and of the overlying layer of ectoderm. This membrane is the forecast of the velum and subsequently will become perforated.

In the most advanced stage observed (fig. 14), the velum no longer extends right across the mouth of the subumbrella cavity, but has broken through in the middle. The tentacles

have increased in number since the previous stage, and the older ones are relatively much longer, so that they hang through the velar aperture into the subumbrella cavity. The tips of some of the tentacles are already provided with cnidoblasts. Also in some of the older tentacles a considerable lumen has made its appearance owing to an axial split in the endoderm. The gastro-vascular system is well developed in this stage. The circular canal is the first to appear as a split in the endoderm at the base of the tentacles, and is soon placed in communication with the enteric cavity of the parent by the four radial canals which arise one opposite to each of the four perradial tentacles. Between the radial canals and all round the "glockenkern" the endoderm persists as the endoderm lamella.

At a very slightly later period the mesoglœa makes its appearance between the endoderm lamella and the ectoderm of the exumbrella, as seen in the horizontal section, fig. 15, *m. s.*

An Abnormality in Bud-formation.

As a rule the Medusa buds are situated on the outer surface of the manubrium of the parent, but on two occasions a bud with free tentacles was found projecting into the stomach cavity. This lusus naturæ in both instances occurred in a region where the buds were more closely packed than usual, and, consequently, as there was not sufficient room for the buds to develop on the outside of the manubrium, they forced their way through the wall of the manubrium and grew into the stomach cavity—only in a reversed condition, just as the young Tænia head grows into the Cysticercus instead of outside it.

As a result, the disposition of the cell layers and organs in such an abnormal bud is completely reversed. The velum develops outside the circlet of tentacles and the subumbrella epithelium becomes external, while the exumbrella epithelium becomes internal. An examination of fig. 16 will make this clear. The endoderm is continuous with the general endoderm

of the manubrium as in a normally developed bud, and so likewise the exumbrella ectoderm is continuous with the manubrial ectoderm. But the ectoderm covering the subumbrella has undergone rupture at the point *x*, and the entire bud has forced its way through the aperture.

The future of these monstrosities must remain a matter of doubt. It would be interesting to know whether such abnormal buds are reabsorbed by the parent or whether they are capable of further growth and are then cast off. In any case it would seem improbable that a Medusa bud in this condition should eventually right itself, in spite of the acknowledged powers of regeneration which are characteristic of the Hydrozoa.

Bud-formation of Limnocnida contrasted with the same process in other Hydrozoa.

If we compare the process of development of Medusa buds in Limnocnida, as detailed above, with the same process in other Hydrozoa, several striking points of difference are noticeable. In the first place the method of invagination of the ectoderm to form the entocodon or "glockenkern" in Limnocnida differs from the method of formation in most other Medusæ in which the process has been described, and I am inclined to think that in this respect Limnocnida exhibits a more primitive condition.

As a general rule we find that in the Craspedota the earlier stages of the development of the Medusa buds, whether they subsequently give rise to free Medusæ or whether they grow into any of the various degenerate modifications of the Medusa, show considerable shortening of their ontogeny. It would be superfluous to recapitulate all the arguments used in favour of this view. Weismann in his monograph on the 'Entstehung der Sexualzellen bei den Hydromedusen' has brought forward abundant evidence to indicate the phylogenetic stages by which the primitive method of the formation of the Medusa-bell by the outgrowth of a circular fold has become changed into a process of invagination.

Examples of this invagination in a more or less modified form have been described and figured in many different genera of Hydroids, but in none does it exhibit quite such a primitive condition as in Limnocnida. In the majority of Hydroids described, the invagination takes the form of an ingrowth of a solid mass of cells, called the "glockenkern." In some cases however, such as Hydractinia echinata, Weismann (15) Taf. xxiii, fig. 5, and better in the young buds of Clava squamata, Taf. v, Galeolaria aurantiaca, Taf. xxi, and Podocoryne carnea, Taf. xix, the "glockenkern" is seen to be hollow in the youngest stages figured, but whether a cavity exists in any Hydroids from the first, or whether it is only subsequently formed as appears in the above cases, remains to be decided by future investigations. In Limnocnida the "glockenkern" is a hollow invagination from the very first, and its cavity becomes shut off from the exterior at a later period, but is typically retained throughout.

The later stages of Limnocnida buds, and especially the formation of the velum from two distinct layers of ectoderm which afterwards break through in the centre, are almost exactly paralleled by Bougainvillea fruticosa and Perigonimus cidaritis (Weismann, Taf. xii, figs. 10, 12, and 13).

A noticeable feature in the development of the Medusa buds of Limnocnida is the entire absence of any trace of manubrium and mouth in any of the stages examined. It is true that in the adult the size of the manubrium is very insignificant as compared with the dimensions it assumes in other Medusæ; but nevertheless its entire absence in the young buds is, to say the least, remarkable. In the development of all other Medusa buds in the Hydrozoa, the manubrium is one of the most conspicuous parts of the young bud, and in the case of degenerate Medusæ its presence is characteristic. The absence of manubrium and mouth in Limnocnida buds is, no doubt, to be accounted for by the fact that the young buds seem to obtain their nutriment direct from the gastric cavity of the parent, and therefore have no need of a mouth or manu-

brium. The mouth probably breaks through at the date of the setting free of the young Medusæ.

II. General Conclusions regarding Systematic Position.

It is perhaps idle to speculate upon the phylogenetic position of Limnocnida, considering that we are in absolute ignorance regarding its mode of development from the egg, or of its life-history, but it is expedient for purposes of reference that all such newly-discovered organisms should be given a place in the system, as natural as the state of knowledge will permit. At the same time any attempt at constructing new groups, or at arranging old ones, to contain a species about which we know as little as of Limnocnida, is to be deprecated on the ground that such a course might add fresh burdens to an already overladen nomenclature.

According to the preceding account the two most important characters known in Limnocnida are, firstly, that the gonads are developed on the walls of the manubrium; and, secondly, that the sense-organs situated on the margin of the umbrella have an endodermal axis. The only known Medusæ which possess these two characters in combination are the Narcomedusæ. On the other hand, Limnocnida possesses hollow tentacles, while those of the Narcomedusæ are solid, though occasionally partly hollow in the adult, and the sense organs of Limnocnida possess no structure corresponding to the otoliths of the Narcomedusæ.

I regret that my acquaintance with the Narcomedusæ does not justify me in expressing an opinion as to whether the association of Limnocnida with them is a natural one or not; but, as Limnocnida has undoubtedly reached the same grade of development in respect to two of the most important features of the group, it is convenient to find a provisional home for Limnocnida in connection with the Narcomedusæ, and to wait until we know more of

its life-history before any attempt is made to fix its abode definitely.

The only fact we have at present about the life-history of the Medusa is that during part of April, May, and June, swarms of male, female, and asexual bud-bearing individuals coexist in Lake Tanganyika. The most important problem to be solved is, Does Limnocnida pass through a fixed hydroid stage in any part of its life-history? Is its development metagenetic or hypogenetic?

It is certainly possible that, as in the case of the Narcomedusæ, there is no fixed hydroid stage. It seems to me conceivable that a kind of alternation of generations may occur in Limnocnida such as has been described by Brooks (3) in Willia ornata (if rightly identified), in which asexual Medusæ produce sexual forms by budding. It is possible that the sexual individuals of Limnocnida may produce eggs which develop into free-swimming planula-larvæ which grow into the asexual Medusæ, which in their turn give rise to sexual Medusæ by budding.

On the other hand, if a fixed hydroid stage form part of the ontogeny, Limnocnida must be separated from the Narcomedusæ which do not pass through such a stage, and then would have to be regarded as descended from an Anthomedusa-like ancestor and as having developed sense-organs with an endodermal axis, just as Limnocodium is to be regarded as a descendant of the Leptomedusæ with sense-organs morphologically similar to those of the Trachomedusæ.

With regard to the striking similarity of the sense-organs in both the fresh-water Medusæ, Limnocodium and Limnocnida, I can only consider it to be another instance of parallel but independent evolution of similar organs in two genera which are not related to one another, but which live under similar conditions ("homoplasy" of Lankester, cited by Darwin, 'Origin of Species,' 6th edit., p. 385). If this is really the case, the similarity of structure is most remarkable.

III.—Fresh-water Medusæ.

The discovery of a new Cœlenterate living in fresh water must always be considered an event of no little importance on account of the fewness of such genera. The chief instances known at present of fresh-water Cœlenterata are the following:—

Various species of Hydra are almost cosmopolitan. They have been described from Egypt (Schmarda), Japan (Hilgendorf), Australia (Bale, von Lendenfeld), and New Zealand (Coughtrey). The allied genus Microhydra is an inhabitant of the New World.

Cordylophora is known from the fresh and brackish waters of England, and of North Germany as far inland as the Tegelsee in Prussia; also from America and Australia (v. Lendenfeld).

Polypodium hydriforme, a parasite of the sturgeon, is a native of the Volga (Ussow).

The habitat of Limnocodium is as yet unfortunately unknown, but there is but little doubt that tropical America is its original home.

Lastly, in 1890 J. von Kennell (9) discovered Halmonises lacustris in Trinidad in a fresh-water lagoon completely shut off from the sea, and flourishing in the midst of such truly fresh-water animals as insect and frog larvæ, Daphnidæ, Naids, Æolosoma, Dero, Clepsine, Planorbis, &c.

In addition to these truly fresh-water Cœlenterates several marine forms can tolerate brackish water, for example Aurelia aurita from the Baltic, and Crambessa Tagi from the mouth of the Tagus, and some others.[1]

While treating of such isolated Medusæ, it may be as well to mention the supposed salt-water Medusa recently drawn attention to by Mr. Sclater (13). This Medusa, of which we have as yet no details, is an inhabitant of Lake Urumiah in Persia. Lake Urumiah has no communication with the sea,

[1] See also observations by the late Professor Moseley, in his 'Naturalist on the "Challenger,"' 2nd edit., p. 236.

and consequently its waters are saline. This Medusa (if Medusa it be) may be descended from fresh-water ancestors.

The first question that naturally occurs to the student of evolution is, How did the fresh-water Medusæ get into fresh water? It is clear that they must either have originated there, or they must have immigrated from the sea. The latter of these alternatives is the only one worthy of consideration, since we are not acquainted with any fresh-water Cœlenterate from which the known lacustrine species could be derived; whereas the sea must always be regarded as the true home and birthplace of Medusæ. If this proposition be accepted, there is no reason why all fresh-water Cœlenterates known at present cannot be regarded as having descended from marine ancestors.

In the first place, the mere fact of the difference of salinity between fresh and salt water does not seem to be an insuperable difficulty in the transition from a marine life to a lacustrine one. The marine forms Aurelia aurita and Crambessa Tagi, already mentioned, often frequent brackish water. The only essential condition is, that the change from salt to fresh water must be very gradual, as any sudden substitution of one for the other causes almost instantaneous death to a soft gelatinous creature like a Medusa, owing to the very violent osmotic action which occurs in animals with a soft skin. Experiments demonstrating this point were made long ago by Beudant, and are described by Semper in his 'Natural Conditions as they affect Animal Life.'

The circumstances under which the postulated slow change of environment might occur are of several kinds. All marine creatures found in fresh water have probably either wandered up rivers from the sea, or have been living in bays or lagoons which have become cut off from the sea by the upheaval of land or by the silting up of the connecting channel, or in some other way familiar to the geologist. In any of the latter cases there may perhaps have been an intermediate epoch when the body of water, completely separated from the sea at low water, was still in connection with the sea at high tide.

When such an isolated volume of water has become completely separated from the sea at all stages of the tide, it is further necessary that the rainfall received in its basin should be in excess of the quantity of water lost by evaporation. Given all these conditions, the salt will gradually be washed out and the water will become fresher and fresher, and those of the original inhabitants of the lagoon or bay which could not accommodate themselves to the changed environment would die, leaving the rest to survive as a fresh-water fauna.

Such are briefly the changes which have probably occurred in the case of Halmonises lacustris, which is the inhabitant of a small fresh-water lagoon removed but a few yards from the seashore itself. Its ancestors probably wandered into a small bay or estuary situated where the fresh-water lagoon is now, but in direct connection with the sea. By the upheaval of the land or by some other cause the estuary became shut off from the sea, and the salt water was gradually flushed out by fresh. In the present case the change must have occurred with sufficient slowness to allow not only Halmonises, but also numerous other marine animals, such as several genera of Polychæta, to become acclimatised to a life in fresh water.

Owing to the proximity of the pool inhabited by Halmonises to the sea, the change is easy to understand. In the case of Limnocnida it is far otherwise.

At the present day Lake Tanganyika, according to the description of Mr. E. C. Hore (8), is situated about twice as far from the west coast of Africa as from the east coast. The lake lies at an altitude of about 2700 feet above the sea level, within a mountainous ring fence encompassing a space of, roughly, 600 miles by 300. The lake itself is situated close under the mountains on the western side of this ring, and some 2000 to 3000 feet below the higher parts of the range. All along this western side is an enormous chasm 400 miles long, with an average width of 20 miles and of great depth, varying from 500 to 1000 feet in the middle. The superfluous waters escape by the Lukuga, which runs through a great break in the mountainous rampart on the west side, and is a tributary

of the Congo. It appears that the level of the lake has become considerably lowered within quite recent times. Such, then, are the main physiographical facts relating to the habitat of Limnocnida.

If Limnocnida were the sole representative of a marine fauna in Lake Tanganyika, it would be a surprising fact enough, but it is associated with other marine forms. Just as in the case of the fauna of the Trinidad lagoon, where we find the sea-sprung Halmonises accompanied by marine Polychæte worms, so in the case of the fauna of Lake Tanganyika Limnocnida is accompanied by several genera of molluscs which are perfectly unique in fresh water, and which would most certainly be described as marine forms were their true habitat unknown.

Mr. Edgar Smith (14) especially draws attention to Tiphobia horei and Neothauma tanganyicense, both of which are quite unlike any genera known from the other Central African lakes, and both of which differ from any other molluscs of fluviatile or lacustrine origin.

The question that now arises is, If these organisms are of marine origin, how did they get into Lake Tanganyika?

The answer is undoubtedly difficult to find. A possible explanation is afforded us by the analogy of the marine guests of the Trinidad lagoon. If geologists, when they know more about the geology of Central Africa than they do at present, will allow us to imagine a state of things when the level of the region of the Great Lakes was more than 2700 feet lower than at the present day, and when the Atlantic Ocean extended over what is now the plain of the Congo, and Lake Tanganyika was a fjord communicating with the ocean, then it would have been possible for the ancestors of Limnocnida, of Tiphobia, Neothauma, and other molluscs, to have wandered into the lake, just as at the present day individuals of the Atlantic fauna wander into the Mediterranean. The lake having thus received its marine population, was probably gradually separated from the sea by the uprising of the land and became an inland salt-water basin. At this stage it was possible for one of two

things to occur. It was possible either that the amount of rainfall received by the lake should be less than the amount of water lost by evaporation, or that it should be greater. In the former case the lake would have gradually become salter and salter, or in the latter case the excess of water would have overflowed the banks and the water of the lake would have undergone a gradual process of freshening owing to the salt water being slowly replaced by fresh. It is possible that both conditions may have obtained at various periods—indeed, within our time the lake has been proved to be in both states of quiescence and of overflow. But on the whole the condition of overflow must have been the rule, because at the present day the water of the lake is described as being "perfectly potable."

This hypothesis of the origin of the marine fauna of Lake Tanganyika may or may not prove to be possible when the geology of the region is known. It is, at any rate in the present state of our ignorance, a possible explanation of the presence of a Medusa in the lake. Should subsequent researches prove its untenability, it will have served its purpose if it should stimulate naturalists to discover but a few facts about the past history of the lake or to discover within its bounds members of other classes of the animal kingdom with marine characteristics, from which a new and better theory may be deduced to account for the remarkable and unique marine character of the present fauna of Lake Tanganyika.

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EXPLANATION OF PLATES 18 & 19,

Illustrating Mr. R. T. Günther's paper "A Further Contribution to the Anatomy of Limnocnida tanganyicæ."

List of Reference Letters.

c. c. Circular canal. *chr.* Chromatin. *cnid.* Thread-cells. *e.* Endothelium. *ect.* Ectoderm. *ect. l.* Ectoderm lamella. *end.* Endoderm. *end. l.* Endoderm lamella. *end. m.* Endoderm of manubrium. *gl.* Glockenkern. *g. v.* Gastro-vascular space. *ms.* Mesoglœa. *n. r.* Nettle-ring. *ov.* Ovum. *r. c.* Radial canal. *s. c.* Subumbrellar cavity. *s. ect.* Ectoderm of sub-umbrella. *sp.* Spermatozoa. *st.* Interstitial cells. *te.* Tentacle. *v.* Velum. *vac.* Vacuole.

Fig. 1.—Tangential section of the margin of the umbrella passing through two of the marginal sense-organs. The knife has just cut off a few of the peripheral cells of the larger marginal organ B. The smaller, immature organ A is seen divided in the median plane. At its base is a large triangular cell (x) thrusting itself through the mesoglœa (*ms.*). The marginal bodies

are seen to be situated in a space surrounded by a definite endothelium (*e.*), which separates the sense-organs from the mass of modified thread-cells composing the nettle-ring (*n. r.*). × 1000. Zeiss, apo. 4 mm., comp. oc. 8, cam. luc.

Fig. 2.—The next section to the one figured in Fig. 1. Sense-organ B is seen in median section, and shows the difference between the granular basal cells and the refringent central cells very well. The mesoglœa (*ms.*) forms a slight cup-like elevation round the base of the sense-capsule. The young sense-organ A is also cut near the median plane, and the mesoglœa is discontinuous between the organ and the endoderm. × 1000. Zeiss, apo. 4 mm., comp. oc. 8, cam. luc.

Fig. 3.—Radial section through the manubrium of a female individual, in the region of the ovary. Ova (*ov.*) in various stages of development are readily distinguishable from the interstitial cells (*st.*) on account of their granular structure. The largest ova contain vacuoles (*vac.*), usually situated on the outer side of the nucleus. Covering all is a limiting epithelium of irregular cells (*ect.*). × 400. Zeiss, apo. 4 mm., comp. oc. 4, cam. luc.

Fig. 4.—Section similar to the one figured in Fig. 3, but from the spermarium of a male individual. The layer of ectoderm cells (*ect.*^{1}) nearest the mesoglœa (*ms.*) gives rise to the cells of the second layer, the nuclei of which are alone visible (*ect.*^{2}), and these in their turn break up to form the sperm-cells themselves (*sp.*) No spermatozoa tails have made their appearance in the stage figured. As in the case of the ovary, the entire organ is enclosed by a limiting membrane (*ect.*^{3}). × 400. Zeiss, apo. 4 mm., comp. oc. 4, cam. luc.

Fig. 5.—Radial section through corner of gastric cavity (*g. c.*) to show the point of junction between the endoderm of the manubrium (*end. m.*), the endoderm of the gastric wall of the umbrella (*end.*), and the endoderm lamella (*end. l.*). All cell-walls disappear at the point of junction of the three layers.

Fig. 6.—Radial section across the circular canal and through the base of an interradial tentacle (*te.*). The lumen of the circular canal (*c. c.*) is continuous with that of the tentacle. The large "endodermal organ" fills up most of the lumen of the circular canal. On the outer side is seen a portion of the nettle-ring (*n. r.*).

Fig. 7.—Multinucleate corpuscles from lumen of the circular and radial canals. *vac.* Vacuole. *chr.* Chromatin. × 1000. Zeiss, apo. 4 mm., comp. oc. 8.

Fig. 8.—Longitudinal section through a Medusa bud in the youngest stage. The bud is a mere hollow outgrowth of the wall of the manubrium, and its cavity (*g. v.*) is directly continuous with the gastro-vascular cavity of the parent.

Fig. 9.—Longitudinal section through a later stage. The glockenkern (*gl.*) has just commenced to invaginate at the tip of the bud.

Fig. 10.—Oblique longitudinal section through a stage in which the invagination of the glockenkern is considerably advanced, and the lips of the aperture of the future subumbrella cavity (*s. c.*) have just commenced to close over. As the section is cut obliquely, the gastro-vascular space has just been missed.

Fig. 11.—Oblique section through a Medusa bud, in which the glockenkern (*gl.*) has sunk into the body of the bud, and has become closed over by an overgrowth of ectoderm. Note the persistence of the future subumbrella cavity in the glockenkern.

Fig. 12.—Longitudinal section through a stage at which the second ectodermal ingrowth has commenced. This takes the form of a solid plug of cells (*ect.*), which has pushed into the glockenkern and rendered it cup-shaped. The lumen of the glockenkern has been squeezed into a mere lamina.

Fig. 13.—Longitudinal section through a considerably later stage. The forecasts of the tentacles (*te.*) have appeared, and the velum (*v.*) is well marked though as yet imperforate. The subumbrella cavity (*s. c.*) is large.

Fig. 14.—A longitudinal section of a bud passing along one of the four radial canals (*r. c.*). The circular canal (*c. c.*) has also appeared in this stage; the velum (*v.*) is now perforate, and the tentacles (eight in number) are now free from one another at the tips, though their bases are still connected by a bridge of ectoderm (*ect.*). Note the thread-cells (*cnid.*) at their tips.

Fig. 15.—Transverse section through a bud at a slightly later stage than the one figured in Fig. 14. The mesoglœa (*ms.*) has begun to be deposited between the exumbrella ectoderm and the endoderm lamella (*end. l.*) Note the four radial canals (*r. c.*) The tentacles have been cut more or less obliquely, and are hanging through the centre of the velum (*v.*)

Fig. 16.—An abnormal bud, in which the layers are reversed and which was found growing into the gastro-vascular cavity of the parent. *ect.* is the exterior ectoderm. The tentacles (*te.*) and velum (*v.*) are hanging into the gastric cavity (*g. v.*). At *x x* are the disconnected rims of ectoderm, which in a normal bud would be joined together to form the centre of the ectodermal lining of the oral region of the subumbrella cavity, but which have here become separated by the growth of the bud, which has in fact grown out through its own mouth.

Figs. 8*a*—14*a* are diagrammatic representations of Figs. 8—14 respectively.

Notes on the Minute Structure of Pelomyxa palustris (Greeff).

By

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With Plates 20 and 21.

While working as a student in the laboratory of the Linacre Professor at Oxford, during the summer term of 1893, the opportunity was given me of examining a considerable number of specimens of the interesting fresh-water Rhizopod Pelomyxa palustris, originally described by Professor Greeff in 1867 as Pelobius, and later discussed by him under its present name in the 'Archiv für mikroscopische Anatomie,' Bd. x, 1874. I was enabled, by the kindness of Professor Lankester (to whom my best thanks are due for affording me the material for these observations, as well as for much valuable advice and assistance), to study more than twenty individuals of P. palustris, both in the living state and by means of sections.

Some points with regard to the minute structure which I was able to make out have not, as far as I am aware, been observed before, and others which had been doubtful have received confirmation. It has therefore seemed desirable to bring forward the results of my observations, as far as they go, with the conclusions I have drawn from them, although one or two of these conclusions must be regarded merely as inferences until verified by further investigation. Most of the sections were cut by the skilled hand of my friend Mr. E. A. Minchin, B.A. (to whom I am much indebted for his kind help), and

some were also stained by him. Others cut by Mr. Minchin were prepared by me, and together we obtained a most instructive series, which I studied very carefully. The figures in the accompanying plate are from drawings I made with the camera under high powers, and illustrate the chief points dealt with in these notes. The stains used were Paul Mayer's new "carmalum" and "paracarmine" ('Mitth. Neapel,' Band x, 1891–3, pp. 489, 491); anilines such as eosin, fuchsin, fuchsin S., orange G., and gentian violet, either alone or in combination; also picro-carmine and hæmatoxylin. The sections varied from 1 to 7 μ in thickness. The only observations of mine which can claim to be new have reference (1) to the appearance of a central mass of doubtful significance in the general protoplasm, (2) to the staining properties of the refringent bodies or "Glanzkörper" of Greeff, and (3) to the perfectly definite jointing staining-reaction of the rod-like bodies (a point suspected but hardly established hitherto), which establish the view that they are bacteria. These points, and others confirmatory of previous observations, are considered separately as follows.

General Structure of the Protoplasm.

The protoplasm of Pelomyxa is well known to be highly vacuolated, and in P. viridis Professor A. G. Bourne ('Quarterly Journal of Microscopical Science,' xxxii, 1891) distinguishes between the large vacuoles, which are comparatively few, and the much more numerous smaller ones which he calls "vesicles," and which, in the species described by him, have chlorophyllogenous contents. The difference in size, though not in colour, between "vacuoles" and "vesicles" obtains in P. palustris, and the numerical proportion of one to the other is much the same. Thus the general character of the protoplasm has been considered as practically identical in the two species. But I was able to make out that, in P. palustris at least, the protoplasm surrounding the vesicles was by no means homogeneous, as stated by Professor Bourne for P. viridis, but showed very distinct structure.

The examination of sections under very high powers lent strong support to the views of Professor Bütschli as to the foam-like structure of protoplasm ('Mikroskopische Schäume,' 1892). I was able to confirm the existence of the very fine vacuolisation described by him (loc. cit., pp. 200 and 216) for P. palustris, which probably occurs also in P. viridis, but, as he suggests, may have escaped Professor Bourne's notice. The vesicles in P. palustris, which corresponded to the smallest seen by Professor Bourne in P. viridis, were easily known by their size as compared with that of the nuclei in both forms; and a foam-like structure, consisting of alveoli of infinitely smaller diameter ($\frac{1}{2}$—1 μ) than these vesicles, was most distinct in many of the sections. Fig. 11 shows this fine alveolar structure with a nucleus and two vesicles for comparison; in fig. 10 it is seen on a larger scale. The strands of protoplasm bounding these smallest alveoli, and also some of the thin strands between the large vacuoles, appeared to me homogeneous, and comparable with the finest pseudopodia of Rhizopods and the finest strands of vegetable protoplasm described by Bütschli (loc. cit., pp. 67, 79). The peripheral radiate alveolar border of Bütschli, said to be characteristic of froths, was clearly distinguishable in some sections (fig. 2), and the radiate alveolar layer described by him is seen in fig. 9, (*a*) round a nucleus, and (*b*) round a refringent body.

Appearance of a Central Mass.

In one individual of Pelomyxa, of which a consecutive series of sections had been cut, a very curious appearance was observable. The animal had been killed with osmic acid, and stained in bulk with carm-alum, a delicate protoplasmic stain. The sections presented a central, more deeply staining, irregularly oval ring of apparently denser protoplasm, which was traceable through many sections. The ring diminished at each end of the series to a small central solid patch of denser protoplasm, and hence apparently represented a more or less spherical or oval mass, reminding one somewhat of a central

capsule. The character of the protoplasm was somewhat different without the ring from that within. External to the ring it was highly vacuolated; from the periphery of the animal inwards areas containing very few nuclei or vacuoles, but consisting almost entirely of small vesicles, extended nearly to the boundary of the ring, in some places running quite up to it. Fig. 1 shows a whole section about the middle of the series, drawn without details, showing merely the general appearance and size of the ring, with the nuclei and largest vacuoles. The dotted regions represent the vesicular areas. The ring itself exhibited the extremely fine alveolar structure above mentioned. Internal to the ring I could make out nothing more than a very finely granular appearance of the protoplasm; alveoli, if present, must have been infinitely small in diameter. Fig. 8 is a high-power view of a portion of the ring; the area marked out by dotted lines is represented on a much larger scale in fig. 10, to show more accurately the character of the alveoli. The capsular appearance was not due to the effect of semi-penetration of the osmic acid used in killing, since an individual treated with the same reagent for the same length of time, but stained with picro-carmine, showed no trace of the structure. Some specimens of P. palustris obtained later, which were killed with alcohol and stained in bulk with carm-alum, showed a slight tendency to the same appearance; there seemed to be a drawing together or central concentration of the protoplasm, though there was no definite ring formed. But these individuals presented, in the living state, quite a different appearance from those examined previously. They were shrunk up into a globular shape, were brownish in colour, and perfectly quiescent, so that on first examination they seemed to be dead. But after they had been under the microscope for a long time, they gradually began to assume a more normal appearance, and very slowly put forth pseudopodia. It was a condition suggesting encystment, but no definite cyst-wall was found. It appeared to me possible that these individuals were in a stage leading on to, or nearly connected with, that seen in the first-mentioned

specimen, and that the quiescent condition may have been preparatory to the production of swarm-spores.

The outward appearance of quiescent individuals certainly seemed somewhat to resemble that described by Greeff (loc. cit.) as preceding reproduction. The protoplasm of all quiescent individuals was filled with sand-particles to such an unusual extent that the cutting of sections was a matter of extreme difficulty.

The "Glanzkörper."

The refringent bodies, or "Glanzkörper" of Greeff, were very numerous in P. palustris. Professor Bourne says he never saw "anything in the protoplasm of P. viridis resembling" them, but it seems to me possible that he might have confounded them with vacuoles of the same size, as in life they were often not easily distinguishable (except by the fact of their extrusion from the body) from these.[1] Nor were they always recognisable in sections when stains such as carm-alum and picrocarmine were used. Alum-carmine, used by Professor Bourne, probably would not show them up either. But I found that they stained very readily and deeply with fuchsin, eosin, dahlia, solution of iodine in potassium iodide, picric acid dissolved in turpentine, and some other stains, and could thus be picked out with beautiful distinctness. With all stains except picric acid in turpentine they appeared perfectly homogeneous, but with the latter reagent they showed plainly a fine granulation, and sometimes contained a small bright crescentic area which might represent a space or cavity in the interior. From my observations I concluded that they were almost certainly either solid structures or filled with a coagulable fluid. Greeff observed the granulation with acetic acid, and found these bodies to become deep brown with iodine. I found a solution of iodine in potassium iodide to have the same effect. He also thought he could sometimes distinguish in the refringent bodies

[1] I am inclined to regard the chlorophyll-bearing "vesicles" of Bourne's P. viridis as equivalent to the "glanzkörper" of P. palustris.—E. R. L.

some kind of contents and a nucleus, but I found no appearance of internal structure other than that described above.

I am inclined to think that he, too, sometimes confounded refringent bodies with vacuoles, since he describes a falling in of the walls of the former which occurred with some reagents, and I found a crenellation of this kind to be very characteristic of the food-vacuoles under certain conditions. The refringent bodies divide by constriction, and in fig. 6 the process is seen near completion. M. Pénard ('Archives des Sciences physiques et naturelles,' tome xix, 1893) says that colouring-matters have little or no effect upon them, and that they are either structureless or contain vacuoles. Possibly he looked upon the crescentic areas as vacuoles, or, as he evidently used different reagents, he may have failed to distinguish the refringent bodies from the food-vacuoles, which generally have contents of some sort.

The Vacuoles.

The vacuoles proper were of two kinds, viz. (1) large non-contractile vacuoles, which did not stain (figs. 2 and 8), and (2) food vacuoles of varying size, which were found with and without contents. These contents in all cases stained freely with carm-alum and picro-carmine, and the vacuoles were further distinguishable by the greater thickness, and often by the crenellation of their walls (fig. 8). The "vesicles" of Professor Bourne, which greatly outnumber the vacuoles, and must be placed apart on account of their having in P. viridis chlorophyllogenous contents, are perhaps, as suggested by Professor Lankester, not to be regarded as "vacuoles," but as corresponding to the glanzkörper of P. palustris.

The Nuclei.

With regard to these I have nothing new to add. The nuclei were lodged in the nodes of the protoplasmic network, and presented, as described by Greeff and others, a finely granular structure with several nucleoli in the middle, and deeply-staining chromatin granules arranged peripherally in

a more or less ring-like fashion. I was not able to detect any appearance of nuclear division. The radiate alveolar layer round the nuclei and refringent bodies has been noticed above.

The Bacteria.

The rod-like bodies found in profusion in Pelomyxa were originally described by Greeff as "crystals," but later observers, firstly Bourne, and after him Pénard (loc. cit.), have been inclined to regard them as symbiotic bacteria. Leidy ('Fresh-water Rhizopods of N. America, 1879') and Greeff both thought they distinguished a "transverse striation" of the rods.

M. Pénard considered the rods as "véritables bactéries." He saw in them "une striation transversale, ou plutôt une apparence de divisions à intervalles réguliers, telles qu'on les trouve dans les algues filamenteuses inférieures." With reagents the rods appeared "nettement divisées en plusieurs parties par des étranglements," or "reduites en quelque sorte à des chapelets, dont les nombres respectifs de grains étaient de 2, 3, ou 4." But he did not make it very clear whether the appearance he saw was one of constriction merely and due to reagents, or jointing, which is rather a different thing. Nor did he state definitely the largest number of divisions seen in a single rod, while his description of some of the longest as "filaments ondulés ou recourbés" rather inclines one to think that some of those he saw might have been really the "algues filamenteuses" to which he compared them, and which are not uncommonly found in the protoplasm of Pelomyxa. The rods, as figured in the plate accompanying M. Pénard's paper, show either transverse striation or a moniliform appearance; the former does not of course amount to jointing, and the latter is very different from anything seen by me.

In a Pelomyxa killed with osmic acid, stained in bulk with carm-alum, and teased up in glycerine, I found that the rods were not constricted, but very distinctly jointed

(fig. 4). I obtained the same result with a specimen treated in the same way, but stained with picro-carmine. In the sections, which were mostly double- or treble-stained with anilines such as eosin, fuchsin, fuchsin S., orange G., and dahlia, the rods were deeply stained, and the jointing could be well seen; in some cases the terminal joint could be seen separating off (fig. 7). The rods were always straight and made up of 2, 3, 4, 6, and sometimes even 9 joints. They were highly refringent, and their refractive index seemed to be nearly the same as that of Canada balsam, since in preparations mounted in the latter medium the rods were difficult to see, while in glycerine they were most distinct. The joints had the shape of long prisms, and in a few of the 6-jointed rods a further transverse division of each joint into two was apparent.

In the living Pelomyxa the rods were frequently thrown out into the water, together with refringent bodies and nuclei, a process evidently abnormal and the result of unfavorable conditions. When thus thrown out, the rods exhibited active movement of a kind which has been considered as possibly molecular (Bourne, loc. cit.), but they also travelled round the periphery of the animal. I could not absolutely satisfy myself that the latter movement might not have been due to currents created in the water by the activity of the pseudopodia. Still, taking all the appearances together, it seemed impossible to doubt that the rods were really bacteria.

My friend and fellow-student Mr. M. D. Hill, of New College, Oxford, undertook to prove this by cultivation of the bacteria in suitable media, and some account of his preliminary investigations, which are not yet completed, are appended here.

With regard to the situation of the bacteria, they were scattered more or less throughout the protoplasm, but were, as stated by Greeff, especially abundant around and adhered thickly to the walls of the refringent bodies. Fig. 7 shows some of the latter cut through at different levels, and here the rods are plainly seen in situ. The rods alone are represented in fig. 12.

New Species.

If further criticism of M. Pénard's observations on Pelomyxa be permissible, it would seem that he has scarcely sufficient grounds for the establishment of a new species (P. beleosteii). He does not mention any definite feature which is not equally characteristic of P. palustris. Size is no criterion, since individuals of P. palustris vary very much in this particular, as also in the presence or absence of sand débris in the protoplasm. The sole real difference appears to be in the structure of the nuclei; but as this also differs in two nuclei from the same animal (according to the figure), and both of these, from their thick walls, size relative to the vesicles, and general appearance, bear far more resemblance to food-vacuoles with contents than to the nuclei of any amœba, it would seem doubtful whether they were really nuclei at all. In a paper published several years ago in the 'Archives Exp. de Zoologie,' Korotneff has given reasons for recognising a second species of Pelomyxa. I have no doubt that the form studied by me is the P. palustris of Greeff.

Addendum.

November 10th, 1893.

In order to furnish, if possible, a conclusive proof of the organic nature of the so-called "rods" of Pelomyxa, Professor Lankester suggested to me that I should attempt to obtain a cultivation of these organisms by means of the usual bacteriological methods. This I did during June, 1893, and the following is a short account of the work.

The investigation was carried on in the laboratory of the Regius Professor of Medicine in the University Museum, with the kind collaboration of Dr. Ritchie, who was then, and is at present, engaged in bacteriological research.

We made a large number of cultivations by teasing up fresh specimens of Pelomyxa in sterilised water, after removing them straight from the pond water in which they were kept,

and "sowing" them in test-tubes containing various media, e.g. blood-serum, beef jelly, bovril, &c. The tubes were kept in the dark at the ordinary temperature of the room, except in some cases where artificial warmth was applied. In all these cases a very mixed culture was obtained, and it was impossible to say whether the growth was derived from the "rods." In one instance, however, we were able to detect a few long bacteria, which probably were those for which we were seeking, but it was found impossible to convince ourselves that this was the case.

Furthermore, at Professor Lankester's suggestion, we tried immersing the animals for a moment, some in dilute corrosive sublimate, others in strong alcohol, in order to kill, if possible, the foreign micro-organisms which would naturally be clinging to the surface of the protoplasm, without injuring those in the interior. Cultures were made in the same way as in the previous experiments, but only one was successful. Here we obtained a pure colony of short rod-like forms, which may have been the "rods" in a more finely divided state than that in which they appear normally in the living Pelomyxa. It is probable that, when supplied with abundant nutriment, the "rods" would break down and multiply so rapidly as not to allow themselves to assume the many-jointed condition which Miss Gould has described.

Other methods were tried, such as the "hanging drop" and "fractional" methods, but where colonies were produced they were of too mixed a character to give conclusive results.

At present, therefore, our results are negative as regards having obtained a demonstrably pure cultivation.

My best thanks are due to Dr. Ritchie for his kindness in putting his apparatus at my disposal, and for his help during the work.

M. D. Hill.

DESCRIPTION OF PLATES 20 & 21,

Illustrating Miss Lilian J. Gould's paper, "Notes on the Minute Structure of Pelomyxa palustris" (Greeff).

FIG. 1.—General view of complete section of Pelomyxa palustris without details. Killed osmic acid, stained in bulk carm-alum. Zeiss, obj. B, comp. oc. 4; camera. *r.* Ring of denser protoplasm. *n.* Nuclei. *v.* Vacuoles. *v. a.* Vesicular area.

FIG. 2.—Portion of section. Killed osmic acid, stained in bulk carm-alum. Zeiss, obj. E, comp. oc. 4; tube at 17 mm. *n.* Nuclei. *v.* Non-staining large vacuoles. *f. v.* Food-vacuoles. *v. v.* Vesicles. *p. r. b.* Peripheral radiate border.

FIG. 3.—Portion of section. Killed osmic, stained carm-alum, fuchsin, and eosin. Zeiss, obj. E, comp. oc. 4; tube not drawn out; camera. *g.* Refringent bodies. *n.* Nuclei. *b.* Bacteria. *s.* Sand and débris. *p. r. b.* Peripheral radiate border. *d.* Diatom.

FIG. 4.—Teased-up portion of P. palustris in glycerine. Killed osmic, stained carm-alum. Zeiss, obj. E, comp. oc. 4; tube not drawn out; camera; *b.* Bacteria. *g.* Refringent bodies. *n.* Nuclei. *pr.* Droplets of protoplasm.

FIG. 5.—Teased-up portion in glycerine. Killed osmic, stained picro-carmine. Zeiss, obj. E, comp. oc. 4; tube not drawn out; camera. *b.* Bacteria. *g.* Refringent bodies. *n.* Nuclei.

FIG. 6.—Portion of section. Killed osmic, stained picro-carmine and picric turpentine. Zeiss, obj. E, comp. oc. 4; tube not drawn out; camera. *g.* Refringent bodies. *g g.* Dividing refringent body. *n.* Nuclei.

FIG. 7.—Refringent bodies, to show rods in situ. Killed osmic, stained picro-carmine and dahlia. Zeiss, oil imm. $\frac{1}{12}$, comp. oc. 4; tube at 17 mm.; camera. *n.* Nuclei. *b.* Bacteria. *g.* Refringent bodies. *w.* Wall of refringent body.

FIG. 8.—Small portion of section, including bit of capsular region. *r r.* Width of ring. *i. pr.* Protoplasm within ring. *e. pr.* Protoplasm external to ring. *f. v.* Food-vacuoles. *sq.* Alveolar area represented in Fig. 10. Killed osmic, stained carm-alum and dahlia. Zeiss, oil imm. $\frac{1}{12}$, comp. oc. 4; tube at 19 mm., finished with comp. oc. 8; camera.

FIG. 9.—A. Nucleus, with surrounding radiate alveolar layer. Killed osmic, stained carm-alum. B. Refringent body, with surrounding radiate

alveolar layer. Killed osmic, stained picro-carmine and picric turpentine. Zeiss, oil imm. $\frac{1}{12}$, comp. oc. 8; tube at 19 mm.; camera.

Fig. 10.—Protoplasm between vacuoles, to show finest alveolar structure. *v*. Vacuoles. *a*. Alveoli.

Fig. 11.—Small portion of section. Killed osmic, stained picro-carmine and hæmatoxylin. Zeiss, oil imm., comp. oc. 8. *n*. Nucleus. *v*. Vacuoles. *v. v*. Vesicles corresponding to the chlorophyllogenous vesicles of P. viridis.

Fig. 12.—Bacteria. Zeiss, oil imm. $\frac{1}{12}$, comp. oc. 4; tube not drawn out.

On Moniligaster grandis, A. G. B., from the Nilgiris, S. India; together with Descriptions of other Species of the Genus Moniligaster.

By

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With Plates 22—28.

External Characters.

Colour and Size.—The general appearance, colour, and size may be judged from figs. 1 and 2. An average-sized worm which I measured was 590 mm. long when living and at rest, 270 mm. when fully contracted, and 1080 mm. when stretched out after having been (purposely) badly preserved.

The most striking feature in the living worm is the great activity of the twelve or fourteen most anterior somites as compared with the extreme sluggishness of the greater portion of the body. When removed from the ground the animal seems to have very little control over all the hinder portion of its body. The body-wall is here very thin and weak, and often becomes ruptured in specimens which are kept in captivity. When this happens the gut instantly bulges out at the point of rupture.[1]

[1] Great differences exist among earthworms with regard to what happens when the body-wall is injured. Some worms, like M. grandis, will live on for a long time with a portion of the gut bulging out, while others, e. g. Perionyx saltans, will, on receiving the slightest injury to the body-wall, breek at once into two pieces. The body-wall behaves in some cases as though

There is very little pigment in the body-wall, which in the greater portion of the animal's length is very transparent, but which becomes opaque at the two extremities. The opacity is due even here rather to the greater amount of muscle present than to the presence of pigment. What little pigment there is occurs in the connective tissue which lies below the epidermis and between the muscle-fibres. There is in Segments x—xiii (the region where the clitellum develops) in all fully-grown worms an orange tint which is due to pigment, and the dorsal region of the anterior segments of a worm which has been killed in spirit presents a greenish appearance which must be due to the alteration in colour of a pigment. When the worm has been preserved in spirit for some time, this coloration passes away.

The coloration of M. grandis depends chiefly upon the earth which it takes into the gut. It almost always occurs here in a light-coloured soil, and is consequently itself light in colour.

Number and Character of the Segments.—The largest number of segments which I have met with is 480, the smallest 266, this in a worm $3\frac{3}{4}$ inches long. One of the most striking features in the external appearance of the worm is the great variation in size of the segments (figs. 1, 2, 15, 16). They increase in both length and circumference from before backwards down to Segment viii, which is the longest in the body. Segments ix and x are of about the same length as one another, but rather shorter than Segment viii. Segments xi, xii, and xiii are each rather shorter than the preceding segment. From Segment xiii there is but very little decrease in the length of the segments, which are all, as compared with most worms, very short relatively to their circumference. The circumference of the body varies so much with the amount of earth in the alimentary canal that one must be very guarded in making any statement respecting it (fig. 1 gives the natural size of a big

it were tough, and in others as though it were brittle, and the end of the worm breaks off on receiving the slightest injury—like the end of a lizard's tail.

worm full of earth), but if a starved worm, from which most of the earth has been voided, is killed by immersion for a few minutes in strong spirit and then stretched, it may be very clearly seen that the body tapers from Segment VIII, gradually but regularly, right away down to the tail end, which is then a blunt point. If such a worm is left in strong spirit until all the muscles have been contracted and become firm and hard, the region immediately in front of the anus becomes swollen out into a knob. I think that this is due to the strong contraction of the thick layer of longitudinal rectal muscles.

This particular shape and this great variation in the size of the segments is not by any means common among earthworms, and does not obtain, for instance, in the majority of Moniligasters.

As a rule the segment is clearly divided into two annuli, while each of these is again obscurely divided (at any rate in about the anterior half of the worm) into two, making in all four annuli (see fig. 15, Segment XV). The setæ are placed upon the second of these four annuli. The fourteen anterior segments are peculiar in their annulation. Segments I, II, and III consist of one annulus only, and Segments IV and V of two annuli only, while in Segments VI—X there are more than the usual number of annuli, but the additional annuli are very irregularly marked and frequently do not extend round the whole circumference. Fig. 3 is accurately drawn from one individual. When the clitellum is developed the annulation in that region disappears, but I have never seen the demarcation between the segments disappear or even become to any great extent obscured.

Prostomium.—This is not dovetailed into the peristomial segment (Segment I), but is very definitely marked off from it by a groove. The anterior edge of the peristomial segment is almost always turned in, so that the prostomium appears to protrude from the buccal cavity. When the prostomium is fully protruded a portion of the buccal membrane is protruded also (see fig. 4). It can be entirely withdrawn, and in spirit specimens is usually invisible (in fig. 15 the prostomium is

entirely withdrawn). It is constantly changing its shape during life. It is hollow, the body-cavity being prolonged into it. Muscles attached to its inner wall and passing backwards to the body-wall serve to withdraw it (see fig. 17), while if cœlomic fluid is forced into it, it becomes much distended.

Setæ.—The setæ are very ordinary in shape (fig. 26), and bluntly pointed at either end. They present no remarkable features, nor do they differ, so far as I can see, to any extent from one another. They are as nearly as possible 0·5 mm. in length; that is to say, they are very small as compared with the setæ of most worms—as small as those of Microchæta. They are arranged in couples, the two setæ in each couple being very near together. In a large-sized specimen which I measured, the circumference at about Segment XXV was 36·5 mm., the dorsal gap 18 mm., the lateral gaps 6·5 mm. each, and the ventral gap 5·5 mm. More anteriorly the dorsal gap increases very slightly at the expense of the lateral gaps.[1]

Both seta couples are, as usual, absent from Segment I; they are also absent in this worm from Segment II, while in Segment III the inner couples alone are present. I have never found any instance of any of the setæ having accidentally fallen out or been lost; and young setæ (soies de remplacement), so common in many worms, do not often occur; I think that they occur at certain particular seasons, when a new set of setæ develop. There are no modified setæ of any kind. The setæ are so small that the position of neither the individual seta nor of the couple can be observed on an inspection of the inner surface of the body-wall. The position of the rows of seta couples is, however, clearly marked by the arrangement of the muscles (see below, Muscular system).

[1] The relative positions of the seta rows are of importance for systematic purposes in this group. My measurements are taken in the following manner: the worm is killed in strong spirit, a ring of the body-wall, consisting of one or two somites, is cut off at about Segment XXV, cut through along one of the seta rows, and then flattened out, avoiding any stretching, and measured.

Clitellum.—A clitellum undoubtedly develops—at a certain restricted time of year—in connection with Segments x, xi, xii, and xiii. It commences, even in the most fully developed specimens which I have seen, on the second annulus of Segment x. It is not developed at all upon the ventral area of Segments x, xi, and xii, and so does not actually include either the male or the oviducal pores, but it is developed over the whole of Segment xiii. Before it becomes recognisable in living specimens, it may be distinguished in a worm which has been placed in spirit for half an hour, as the future clitellar area then becomes orange-coloured.

Mouth.—The mouth is ordinarily completely occluded by the retracted prostomium, but it is capable of great distension. From time to time the worm protrudes the prostomium and the whole of the buccal membrane, and, indeed, the whole of the dorsal wall of the pharynx.

Anus.—The anus is a narrow vertical slit.

Dorsal pores.—There are no dorsal pores.

Nephridiopores.—These are very easily seen. There is a pair in every segment, except Segments i and ii and the two most posterior segments. They are all placed close to the intersegmental groove, but upon the anterior portion of the segment in which the nephridium lies. The seven most anterior pairs of nephridiopores, i. e. those of the nephridia of Segments iii—ix, lie to an equal extent dorsad of the outer seta row. The remaining pores lie exactly in the outer seta row.[1]

Genital Apertures.—There are three pairs of genital apertures, all strictly intersegmental, and lying between Segments vii-viii, x-xi, and xi-xii respectively.

The male pores lie between Segments x-xii, and slightly dorsad of the inner seta couple. They are large oval apertures, and the immediately adjacent annuli form concentric lips (fig. 15), and the surface is here and in the immediate neighbour-

[1] This peculiar arrangement shows how careful it is necessary to be in describing the position of nephridiopores, especially in spirit specimens, where it is often very difficult to see them at all.

hood much corrugated. Sometimes after the animal has been killed in spirit a conical papilla is formed, at the top of which lies the actual pore. No other papillæ are ever found in this region.

The oviducal pores lie between Segments XI and XII, slightly nearer the median ventral line than the male pores, and therefore almost exactly in the direction of the inner seta couples (fig. 15). The pores are exceedingly minute, and are indeed hardly recognisable. The corrugations of the surface above mentioned extend as far as the oviducal pores (fig. 15).

The spermathecal pores lie between Segments VII and VIII, and very slightly ventrad of the outer seta row. They are easily recognisable, and appear to lie upon a little eye-shaped piece of tissue which is inserted between the two segments (figs. 15 and 16). Here, as in the case of the male pores, little papillæ may stand out with the pore upon the apex.

Body-wall, Body-cavity, and Septa—Muscular System.

Body-wall.—The body-wall is very thick in the anterior region, but is everywhere else very thin compared to what it is in many worms.

The cuticle presents the usual characters.

The structure of the epidermis is very clear and distinct. Five kinds of cells occur in the epidermis—ordinary epidermic cells, sensory cells, and three kinds of gland-cells, viz. (1) goblet-cells, (2) short club-shaped cells, and (3) long club-shaped cells.

Setting aside the sensory cells, it is only necessary to distinguish between the clitellar segments and the non-clitellar segments or main portion of the worm.

In a non-clitellar segment the only glands present are the goblet-cells (fig. 18, *gob.*). These occur in great numbers in the middle of the segment, but are absent from the intersegmental grooves (fig. 59). They are as numerous in the interannular grooves as elsewhere. The ordinary cells are rather shorter in the intersegmental grooves than elsewhere, and

strictly columnar in shape. Those cells which are packed between the goblet-cells are—at any rate when the goblet-cells are full of secretion—much pressed out of shape. In many of my sections the goblet-cells are extremely distended, but they never dip down below the ordinary epidermic layer. The nucleus is pushed right down to the base of the cell. The secretion does not become stained on treatment with alum carmine. These cells correspond apparently to the finely granulated cells of Lumbricus,[1] and they are the only gland-cells present, there being no cells in a non-clitellar segment corresponding to the coarsely granulated cells of Lumbricus. I have recognised these two kinds of gland-cells in a good many genera, including Lumbricus, but it is very clear that only one kind is present in M. grandis, or, I believe, any Moniligaster.

The clitellum, as stated above, develops upon Segments X, XI, XII, and XIII, but not upon the whole of Segments X, XI, and XII, so that in the clitellar region we have to distinguish between clitellar epidermis and non-clitellar epidermis, and there is further a difference between the epidermis in the neighbourhood of the genital apertures and the rest of the non-clitellar epidermis.

In the clitellar epidermis (fig. 19) ordinary epidermic-cells and goblet-cells occur, and in addition to these the two other kinds of gland-cells mentioned above. The ordinary cells and the goblet-cells form a surface layer through which pass the necks of the other gland-cells. The main portions of what I have called above the short club-shaped cells form a distinct layer of more than twice the thickness of the superficial layer. These short club-shaped cells (figs. 19, *s. cl.*) are filled with large granules which stain deeply with alum carmine, and correspond, I believe, to the coarsely granulated cells of Lumbricus. The innermost layer of the clitellum, a layer which is thicker than the other two layers together, is made up of the main portions of the long club-shaped cells (fig. 19, *l. cl.*), so that some of these, the ones that dip furthest down,

[1] Cf. Cerfontaine, 'Arch. de Biologie,' t. x, 1890.

are very long indeed. Their contents are finely granular, and do not stain with alum carmine. Connective tissue runs up between these cells, and tends to separate them into groups. Such cells appear to exist in the clitellum of all worms, and not elsewhere, so that they are probably the true clitellar glands, and secrete the egg-capsule.

The epidermis in the neighbourhood of the genital apertures consists of columnar cells which are rather thinner and longer than those elsewhere, but none of them have become glandular (fig. 20). In the other non-clitellar portions of the clitellar region, the epidermis is similar to that found in the clitellum proper, except that the long club-shaped cells are entirely absent, and the short club-shaped cells are rather shorter. These cells, which are very clearly confined to the clitellar region of M. grandis, are found all over the body in many other worms, and it is difficult to assign a function to them. As our Moniligaster needs to have the surface of its body kept moist with mucus (it lives in what is often very dry earth), and the only glands present all over are the goblet-cells, we may assign to them a mucus-secreting function, a theory which is borne out by their appearance, and as the only glands which seem to be always confined to the clitellum are the long club-shaped glands, we may assign to these a capsule-secreting function—but what is the function of these coarsely granulated glands?

Capillary blood-vessels are remarkably abundant in all Moniligasters throughout the epidermis.

The usual circular and longitudinal muscular layers of the body-wall are present. The circular muscles form, as Cerfontaine has pointed out for Lumbricus, an almost continuous sheath, thickest towards the middle of a segment and thinnest in the region of the intersegmental grooves, and interrupted only for the passage of the setæ, excretory ducts of the nephridia and generative organs, and the muscles of the setæ, &c.

The muscle-fibres are unlike those of Lumbricus and most worms. They are like those of a leech, each cell having

a superficial layer of contractile substance, while the medullary portion consists of unmodified protoplasm and contains the nucleus.

The longitudinal muscles form four longitudinal bands running the whole length of the body. The dorsal band is semicylindrical, extending over, as nearly as possible, half the body-wall. The ventral band is the narrowest; it lies between the inner rows of seta couples, while the lateral bands lie on each side between the inner and outer rows of seta couples. As the setæ are so small that they do not project through the body-wall, and the two setæ in a couple so near together, there are no intersetal or accessory bands such as are present in Lumbricus. Each band is built up of a number of bundles of cells. There is no bipinnate arrangement, the cells in each bundle form a solid block. The bundles lie very close to one another, there being only a very small amount of connective tissue present, and this has the nature of a granular stroma.

The parietal layer of cœlomic epithelium has the usual character.

Septa.—Four of the septa are very thick, viz. v-vi, vi-vii, vii-viii, and viii-ix; the remainder are all very thin and do not vary[1] in thickness, excepting that towards the anal end of the body they become gradually thicker.

The thin septa are very thin and absolutely transparent when fresh, and remain fairly so even in spirit.

The arrangement of the septa in the anterior region and the consequent location of various organs has given me a good deal of trouble. The safest guide to the numbering of the various segments is to be found in the efferent ducts of the nephridia, which can with care be always traced with certainty up to the point where they penetrate the body-wall. The nerves arising from the ventral nerve-cord are also useful for purposes of enumeration, as they come off with absolute

[1] I note this in contradistinction to the condition of many worms, where the septa which follow the thickened septa become gradually thinner and thinner. Here the transition is perfectly sudden, Septum viii–ix is the thickest, and Septum ix–x is as thin as any other, in the body.

regularity (figs. 27 and 49). Without careful attention to these points one might be very easily led into error. The setæ are so small that unless well protruded they are often not visible in the anterior region, where the body-wall is so thick, and the annular grooves are in places so pronounced, that from an inspection of the cut edge of the body-wall it is impossible to say with certainty which grooves serve as demarcations between neighbouring segments and which between neighbouring annuli only.

It is well known that in some worms certain of the septa may be absent, but here all the septa are present, only some become displaced; and I need hardly say that in all cases the septa should be numbered with regard to their relation to such organs as occur in continuous series (e. g. nerve-branches, nephridial ducts), rather than with regard to the position of their attachment to the body-wall.

The four thickened septa above mentioned join the body-wall in the region of the intersegmental grooves, the most anterior, v-vi, showing, however, a tendency to run a little forward along the body-wall.

I can recognise three structures in front of these which might be the septa ii-iii, iii-iv, and iv-v, but these are attached (see fig. 17) to Septum v-vi, and never reach the body-wall, and are therefore not septa, but special mesenteries supporting the nephridia, such as are connected with the other nephridia (see below).

The only septa with regard to which there is any real difficulty are ix-x, x-xi, and xi-xii.

Septum ix-x is attached to the body-wall in the dorsal region near the intersegmental groove x-xi, while in the ventral region it is attached in its normal position. This is the septum which supports the seminal capsule, and through which the vas deferens passes. At the spot where the excretory duct of the nephridium of Segment x penetrates the body-wall, this segment is carried forward so as to leave nephridium 10—i. e. the nephridium of Segment x—entirely behind it.

Septum x-xi is the most modified; the greater portion of it

is in an adult worm so arranged as to reduce the (body) cavity of Segment XI to two sacs; one of these contains the ovaries and nephridia of the segment, and into it the oviducts open internally (the oviducts are, as a matter of fact, mere modifications of a portion of the wall of this segment); the other sac contains the portions of the dorsal vessel, the alimentary canal, and the ventral vessel, which belong properly to the segment. The portion of this septum which forms the latter of the above-mentioned sacs does not touch the body-wall at all; the portion forming the sac containing the ovaries, &c., joins the body-wall along a small portion of the ventral region only; elsewhere it is attached to the septum which follows, viz. XI-XII. The nerve-cord does not lie in any portion of its course in the cavity of Segment XI; there is a free passage through from Segment X to Segment XII. (See the arrow in fig. 27, and note also in this figure the arrangement of this septum in relation to the duct of the nephridium of this segment.) The cavity of Segment XI only passes forward to its proper limit as a cæcal prolongation surrounding the nephridial duct.

Septum XI-XII is attached to the body-wall in the normal position, and is only peculiar in being prolonged backwards to form the wall of the receptaculum ovorum (figs. 17 and 59).

The remaining septa are normally attached; those of the three or more segments following XI-XII get pushed back by the receptaculum ovorum on each side, the number of septa thus displaced depending on the time of year, i. e. the state of the development of the receptaculum ovorum; but when this is fully developed it may rupture some of the septa; further, those septa in the neighbourhood of the gizzard become much displaced where they surround the alimentary canal, as they must be, considering that the gizzard region when extended occupies 35 mm., while the five segments containing it measure when contracted only about 5 mm. in length.

The relation of the septum to the chief organs which run a longitudinal course from segment to segment is indicated in fig. 13, from which it will be seen that the septum is in actual

contact with the dorsal vessel, intestine, ventral vessel, and the lateral longitudinal vessels (only in the region where these exist of course), the nerve-cord itself runs freely through the septa, there being a space left all round through which the cavity of one segment communicates with that of the adjacent segments.

Mesenteries.—I apply this term (it is using the word in a forced sense) to a set of mesentery-like structures which attach various organs to one another or to the body-wall (fig. 41). In the interseptal regions the dorsal vessel and the ventral vessel are each attached by a longitudinal mesentery to the intestinal wall, so that these three structures run through the segment attached to one another, but not attached to any other structures. The lateral longitudinal vessels are attached, along their whole course through each segment in which they occur, to the body-wall in the ventral region by longitudinal mesenteries, but are otherwise unattached. The line of attachment of these last-mentioned mesenteries begins on the hinder surface of the septum near the middle line, at the level of the dorsal vessel, and passes along the septum outwards and downwards and then inwards, curving round to the inner seta line, and then back along the wall of the segment just inside the inner seta line, and then up on the anterior face of the hinder septum of the segment in which they lie towards the dorsal vessel. Prolongations from these mesenteries hold the nephridia, the hearts, and where necessary the spermathecæ and their ducts, and the vasa deferentia.

Behind the region of the lateral longitudinal vessels, and therefore of these special mesenteries, there are much smaller mesenteries attaching the nephridia to the posterior face of each septum.

All the septa and these mesenteries are lined on both sides with irregularly-shaped pavement-epithelium cells. The thin septa consist of little else, a few straggling muscular fibres and a little connective tissue, but the four specially thickened septa and the septa in the posterior region of the body contain a much larger amount of muscle; on each surface there is a layer of centripetally placed fibres, while the main mass of the

septum is made up of fibres crossing one another in all directions. Where the septum joins the body-wall the centripetally placed fibres spread out and penetrate to a certain extent the longitudinal muscular layer of the body-wall. In the case of the septa in the hinder region the same sort of thing occurs at the junction of the septum with the intestinal wall, indeed, close to the intestinal wall the septa become so thick as to almost join one another along the intestinal wall.

Alimentary Tract.

It is, so far as I can see, impossible to say with certainty from an examination of the adult worm, to what segments the anterior portions of the alimentary canal really belong. In front of Septum v-vi, i. e. in the five most anterior segments, lie the buccal region, the pharynx, and a considerable length of œsophagus. From the arrangement of the nephridia and blood-vessels I should say that this latter occupies, at any rate, Segments iii, iv, and v; this leaves Segments i and ii only for the buccal region and pharynx. Longitudinal sections show a slight change in the character of the alimentary epithelium at the posterior limit of Segment i, so that I think we may assume that the buccal region occupies this segment while the pharynx is confined to Segment ii. The pharynx extends backwards, of course, far beyond the limits of this segment as marked by the grooves on the body-wall, but these, as we know, by no means determine the true anatomical position of an organ.

The buccal region is completely eversible and can be protruded with the prostomium (fig. 16), or it can even be protruded while the prostomium remains completely withdrawn.

The pharynx is comparatively thin-walled except in the dorsal region. When the pharynx is cut open ventrally a circular portion of its dorsal wall appears as a thick pad, while a circular wall stands up all round this. This pad can be protruded, and forms the piston which is used in sucking in the earth and in excavating the burrows (fig. 17, *m.*). Numerous strong muscles run from the outer wall of the pharynx to

the body-wall, but those which serve to retract this pad are much stronger than any of the others, and are attached as far back as the wall of Segment VII. The œsophagus really opens into the ventral wall of the cavity of the pharynx, so that this latter might be regarded as a diverticulum of the dorsal wall of the œsophagus. The œsophagus is very straight and narrow, slightly constricted at the septal regions, and does not change its character in any way until Segment XV. The walls throughout are much firmer and stronger, although no thicker, than the œsophageal walls in, for instance, Megascolex cœruleus. There is really more muscle present in them.

When the other organs and the greater part of the septa are dissected away, it becomes clear that there is a segment of œsophagus belonging to each segment of the body, although, owing to the peculiar arrangement of Septum X and XI, the portion of œsophagus belonging to Segment XI might be easily overlooked, as it is completely enclosed. In Segments XV, XVI, and XVII the œsophagus gradually dilates and its walls become a little thicker. In Segment XVIII is the first of the series of gizzards. There are five gizzards belonging to as many successive segments, i. e. the most anterior gizzard lies between Septa XVII-XVIII and XVIII-XIX and the most posterior between Septa XXI-XXII and XXII-XXIII (fig. 22).[1] The gizzards differ very little from one another, that in Segment XVIII is slightly smaller than the other four. The arrangement which obtains in each of these gizzard segments is as follows:—Immediately following the septum comes the gizzard itself; this is fairly globular in form, the greater part of its wall consisting of a ring of circularly-disposed muscle; this ring of muscle is oval in longitudinal section, so that the lumen of the gizzard is smallest in the centre. Following the gizzard itself is a cylindrical tubular portion of the œsophagus which joins that gizzard to the next following gizzard. Lastly, there are a

[1] It is especially necessary to insist upon this point, because Benham's diagram (11), p. 295, would lead one to suspect a different arrangement. The gizzards should have been shown as they are in Perissogaster, Trigaster, or Hormogaster.

number of bands of muscle attached round the outside of the anterior portion of the gizzard, free along their length, and inserted into the cylindrical portion of the œsophagus in the region of the septum (fig. 23).

In Segment XXIII the wall still remains firm and tough. In the ten segments, XXIV to XXXIII, lies the portion of the canal which corresponds to the tubular intestine of other worms. In the whole of this region there lies embedded in the thickness of the mucous membrane an enormous number of tubular glands, the apertures of which may be seen with a strong lens as little round holes on the surface of the mucous membrane. I have generally found this portion of the canal empty and much shrunk, and consequently immediately obvious, being smaller than the region which follows, but I have found it full of earth and distended, in which case it looks from the outside just like the rest of the intestine.

The "saccular" intestine is very slightly constricted by the septa, and changes very little in character throughout its whole length. In about the last eighty segments its walls become rather stronger, and its blood-supply becomes much diminished; we may term this the rectal region.

There is no typhlosole.

The alimentary epithelium consists in the buccal region of small columnar cells very closely set, and there are no glands. In the pharynx, in the epithelial layer covering the protrusible dorsal wall there are no glands, but between the ordinary cells the salivary glands open in immense numbers. These salivary glands are obviously masses of epithelial cells which have taken up a deep-lying position and a grouped arrangement, but each cell retains its connection with the surface, and pours out its secretion into the pharynx. These salivary glands, which are thin masses of unicellular glands, lie upon the bands of muscle which connect the pharyngeal wall with the body-wall. There are four pairs of such masses lying immediately anterior to such muscle bands, and a much larger median mass lying immediately behind the pharynx (fig. 17). In the epithelium of the ventral wall of the pharynx there is an enormous number

of goblet-cells, looking very like those in the epidermis and probably secreting mucus.[1]

The epithelial cells of the œsophagus are also many of them glandular, and the layer remains unchanged until we reach the gizzard. There the cells become very short, small, cylindrical cells, very closely set together; and here there is a cuticle and no glands. This cuticle is continuous from one end of the gizzard region to the other, but varies in thickness, becoming very thick in the middle of each gizzard and thinning out at either end, being thinnest in the cylindrical regions between the gizzards.

In one segment behind the gizzard there are no glands in the epithelium, and then comes the region of tubular glands. In this region the epithelium on the surface appears only slightly glandular. In a section passing through the aperture of a tubular gland (fig. 24) the ordinary epithelium is seen to be continued some way down the follicle, and then its character gradually changes, the cells become broader and evidently glandular, but they do not become goblet-shaped, and they are all alike; their nuclei are smaller than those of the ordinary epithelial cells. The follicles run straight down to the basement membrane, and then branch and coil.

In the saccular region of the intestine the mucous membrane becomes thin again, and consists of a single layer of epithelial cells only. Most of these have granular contents and appear to be glandular, but they do not become much swollen, or at any rate are not so in any of my sections, which come from several different worms.

In the rectal region the cells are all narrow and non-glandular. Longitudinal sections passing through the anus show that there is no sharp demarcation between rectal epithelium and epidermis.

Of the special muscles of the pharynx and gizzards I have already spoken. In the wall of the rest of the œsophagus and of the intestine the usual muscles are present, a very thin layer

[1] These glands show best when the tissue has been prepared in Flemming's mixture of chromic, osmic, and acetic acids.

of longitudinal muscle, and below that an equally thin layer of circular muscle; in both cases there are scattered fibres rather than a regular layer. In the intestinal wall there are fairly strong longitudinal bands in the median dorsal and ventral walls. Further, in this region, to an extent which increases from before backwards, the muscle fibres of the septa spread out circularly round the outside of the intestinal wall. These fibres lie outside the cœlomic epithelium, and in the rectal region the circular muscular bands so formed become so broad as to be almost continuous (figs. 25).

The cœlomic epithelium of the intestinal region presents the usual characters.

Vascular System.

Having had a practically unlimited supply of fresh specimens, I have been able to work out this system in considerable detail. There is no doubt but that the system has become very fully developed; in dissections, in sections, and in other microscopic preparations I have again and again seen most exquisite "capillary" networks. I have also procured admirable injections for dissecting purposes by injecting a mixture of any very soluble oil paint dissolved in turpentine. This mixture is very excellent in one way, viz. that when the injected specimen is plunged into spirit loose drops of injection at once separate, leaving the specimen quite clean.

Dorsal Vessel.—The dorsal vessel extends from the anterior portion of the pharynx to the last segment of the body. It lies above the alimentary canal, and is adherent along its whole length to the wall of this organ. For the greater part of its length it appears to be actually attached to the intestinal wall, but anteriorly (in the region of the gizzards and in front of them) the nature of the attachment becomes clear, and the latter is seen to be due to the presence of a longitudinal double fold of mesentery (fig. 41), so that it is nowhere possible to put a needle under the dorsal vessel without piercing this mesentery. There is no mesentery connecting it with the dorsal region of the body-wall.

Its walls are muscular throughout its length, and in the anterior segments the cœlomic epithelium covering it becomes pigmented; this is more especially the case near the septa and at the sides.

It is nowhere much dilated, but is largest in Segments VI—IX, and constricted in the region of Septa V-VI, VI-VII, VII-VIII, and VIII-IX (the thick septa). In front of Septum V-VI it very rapidly narrows, and becomes a mere thread on the surface of the pharynx where it dips down among the salivary glands. It does not appear to have any special mode of termination at this anterior end, but simply loses itself in a fine capillary network.

It presents a series of valves (fig. 39) as in Megascolex cœruleus.[1] The valves are placed in the septal regions and prevent any backward flow. There are also valves (mentioned below) at the orifices of the dorso-intestinal vessels.

It is never double in any part of its course.

Posteriorly it ends by dividing into a pair of dorso-tegumentary branches.

Ventral Vessel.—(Fig. 27, V. V.) This is also known as the subintestinal or supra-neural vessel.

Its walls are thick and strong, but are formed of connective tissue and not muscle.

There are no valves in the ventral vessel.

It is of uniform calibre for the greater portion of its length, but posteriorly it gets very gradually smaller and smaller, while anteriorly it narrows rapidly in front of the hearts.

It comes to an end anteriorly and posteriorly by dividing into a pair of branches in each case, those at its anterior extremity lying on the subœsophageal ganglion.

Supra-intestinal vessels are absent.

Typhlosolar Vessel.—No such vessel exists, there being, as I have stated above, no typhlosole.

Latero-longitudinal and Subneural System.—Intestino-tegumentary vessels, i. e. vessels carrying blood between the peripheral capillary networks and the intestinal capillary

[1] Cf. Bourne, 'Quart. Journ. Micr. Sci.,' vol. xxxii, Pl. ix, fig. 12, A.

networks, are not present in any region of the body. "Latero-longitudinal" vessels are very obvious in the anterior segments, from Segment x forwards to Segment v. They are the main trunks, in the anterior region of the body, of a system of vessels of which the subneural vessel is the main trunk in the posterior region of the body. This system must be dealt with as a whole.

This system is connected on the one hand with capillary networks, and on the other with the hearts of Segment IX. It is, in fact, a venous (using the word in an anatomical sense) system for the greater portion of the body. The only capillary networks with which vessels of this system do not communicate, from which, in fact, they do not carry blood back to the hearts, are the capillary networks of the intestinal wall from Segment XIII backwards.

Each latero-longitudinal trunk may be divided, for purposes of description, into three parts, an anterior trunk and a pair of posterior trunks. These come together in the anterior portion of Segment x, unite into a common trunk which passes through Septum IX-X and opens on each side into the heart, or, rather, the neck of the heart of Segment IX. These trunks belong to the cephalised region. The subneural vessel exists along the greater portion of the length of the body. It is the longitudinal vessel into which open all the vessels coming from the capillary networks of the body-wall, septa, and nephridia of all the segments posterior to the cephalised region. It comes to an end anteriorly in about Segment XIV in a very indefinite manner, but all the blood brought forwards by it finds its way into one of the posterior trunks of the latero-longitudinal vessel on each side by such vessels as *a.*, *b.*, fig. 27; the exact arrangement is liable to individual variation. This strikes one as a very inefficient way of disposing of so much blood, but the circulation is here, as in all veins, comparatively slow, and there can be very little blood-pressure; and, besides, the whole circulation in Moniligaster grandis is but feebly carried on in the hinder portion of the worm. It is interesting to recall in this connection

the extreme sluggishness of the hinder end of the worm, and to contrast this state of things with that which obtains in, for instance, M. ophidioïdes, M. robustus, and M. sapphirinaoïdes, where, coexisting with a much more active body throughout its entire length, there is a much more definite connection between the subneural vessel and one of the posterior longitudinal trunks (fig. 29).

There are no latero-neural vessels.

It will be convenient to defer for the present the description of the various branches of this latero-longitudinal and subneural system.

Hearts (figs. 27, 32, and 33).—There are four pairs of hearts, and these belong to Segments VI, VII, VIII, and IX. There is in some worms a little difficulty in determining whether certain particular branches of the dorsal vessel should be regarded as hearts or not. In Moniligaster there is no such difficulty. In all the species which I have examined there are four pairs of hearts and four only.

Their walls are so muscular that when spirit is poured upon a freshly-opened worm the walls of the hearts become so opaque that their red contents can no longer be seen, while the well-developed network of vasa vasorum (fig. 32) supplying their walls comes very clearly into view. The walls of the dorsal vessel also become opaque under similar conditions, only to a very much less degree. In no other vessels of the body are the contents in the least degree obscured by the action of the spirit, nor do I know any other worm in which this phenomenon occurs to anything like the same degree, even in the hearts, as in Moniligaster grandis.

The three anterior pairs of hearts are very simply connected with the dorsal vessel (fig. 32). There is a short narrow neck, and at the junction of this with the dilated heart there is a sphincter muscle. The hearts stand out well from the walls of the œsophagus, but each is attached to the wall along its whole length by a double fold of mesentery.

The hearts of the most posterior pairs have necks at their upper extremities similar to those of the more anterior pairs,

but these are connected one with the other across the middle line, and a short median vessel puts them in connection with the dorsal vessel, while into the necks open the two main trunks of the latero-longitudinal subneural system (fig. 33).

At the lower (or distal) extremity each heart opens into a bulb, between which and the heart proper is a sphincter muscle. This bulb opens directly into the ventral vessel in the case of the three anterior pairs of hearts, but with the intervention of a short neck in the case of the most posterior pair of hearts (fig. 33).

Capillary Networks.—These may be spoken of as peripheral networks and intestinal networks.

Peripheral Networks.—Under this term I include not only the capillary networks of the body-wall and septa, but those of the nephridia, generative organs, walls of the large blood-vessels (dorsal vessel and hearts), and, indeed, those of all the viscera with the exception of the intestinal walls; the capillaries of these latter are really central as compared with the others, but are conveniently termed intestinal networks.

The peripheral networks are extremely well developed throughout, the capillaries being always perfectly clear and distinct. The smallest capillaries measure not more than $\frac{1}{7000}$ of an inch in diameter. There is no trace of any lacunar structure.

There is a sort of fascination in following out these exquisite networks, and I have spent much time in so doing, but it would serve no purpose to describe them in detail. I merely mention this to emphasise the fact that figs. 35—37 are no imaginary diagrams, but accurate drawings of actual preparations. Perhaps the most striking feature of these networks is the strict parallelism which obtains throughout between "artery" and "vein." They are not, indeed, strictly speaking, networks; each small "artery" loops round and becomes a small "vein."

In dealing with Megascolex cœruleus I had only a scanty supply of specimens, and was consequently unable to study these capillary networks in such detail. I used the term

"triple connections" and imagined that networks of capillaries existed in certain places, to which blood was brought by branches of both the dorsal and ventral vessels, and from which blood was carried away by branches of intestino-tegumentary vessels. I am now convinced (from a re-examination of my preparations of Megascolex cœruleus and a study of fresh preparations made for the purpose from another large Perichæte) that this is not the case. I still believe it to be perfectly true that blood carried outwards from the dorsal and ventral vessels passes into intestino-tegumentary vessels, but in one place small capillaries from the dorsal vessel loop over into some branches of an intestino-tegumentary vessel, and in other places small capillaries from the ventral vessel loop over into other branches of the same vessel.[1]

Intestinal Networks.—There is not quite so elaborate a system of blood-vessels in the walls of the alimentary canal as in Megascolex cœruleus, and there is not in a sense the same interest attaching to them as in that form, because their relations to the main trunks are much simpler. The intestinal networks are in the greater portion of the canal (from Segment XIV backwards) directly connected with the dorsal vessel on the one hand and the ventral vessel on the other. There are no vessels having the relations of the intestino-tegumentary vessels of Megascolex; there are, indeed, no vessels communicating at both extremities with capillary networks.

In the anterior region, as far down as Segment XIII, blood is carried to the canal wall by branches of the ventral vessel (ventro-intestinal vessels), and taken away by vessels which run into the anterior longitudinal vessels in the rest of the worm; there are similar afferent vessels, but the efferent vessels run into the dorsal vessel direct (dorso-intestinal vessels). The intestinal networks are best developed in the absorbent region. There the main vessels of the network run

[1] I have been unable to find any account in the literature at my command of the exact connections between the ultimate ramifications of the hepatic artery, the portal vein, and the hepatic vein, in the Vertebrate liver. It would be interesting to know if we have to do here with true "triple connections."

circularly round the intestinal wall. These circular vessels lie very close together, and are connected with one another at short intervals by longitudinally-running junctions, the whole forming a rectangular meshwork. In the dorsal region these circular vessels join together to form the dorso-intestinal vessel in each segment. They take their origin from a network which runs longitudinally along the ventral surface of the intestinal wall on each side of the ventral median muscular band. As part of this network there is a small longitudinal vessel on each side which runs right on from segment to segment; from this there runs in the region of each septum a small circular vessel, lying on the outer wall of the intestine, to the dorsal region. When nearly arrived there it bifurcates, and one branch runs over the intestine and under the dorsal vessel and joins its fellow of the opposite side, while the other is connected with a longitudinal network which lies on either side of the dorsal median muscular band, and which is continuous from segment to segment. In this way provision is made in every segment for communication between the networks of the two sides, and by means of the networks, for communication between the blood supply of one segment and that of another. The ventro-intestinal vessels open into dorsal longitudinal networks on each side.

Dorso-intestinal Vessels.—These are the branches of the dorsal vessel mentioned above which place it in connection with the intestinal capillary networks. They are the efferent vessels of these networks, and the only vessels which bring blood into the dorsal vessel. The most anterior pair are in Segment XIII, and behind these there is one pair in each segment. They are joined to the dorsal vessel immediately behind the septum, i. e. in the most anterior portion of the segment, and each is formed of from ten to twenty branches, all of which spring from the intestinal wall. At the junction of each with the dorsal vessel is a valve precisely similar to that of Megascolex cœruleus, which must effectually prevent any blood passing outwards into it from the dorsal vessel (fig. 39).

These vessels and their main branches are covered, as is frequently the case, with yellowish-brown cœlomic epithelium cells, which make them look very large and very different from the other branches of the dorsal vessel (dorso-tegumentary vessels) which are not covered by pigmented cells.

The connection of these dorso-intestinal vessels with the intestinal capillaries has been described above.

Ventro-intestinal Vessels.—These are branches of the ventral vessel running from it to the intestinal walls. There is one pair in every segment from Segment VI (at any rate) backwards, arising immediately posterior to the septum, except in Segments VI, VII, VIII, and IX, where they arise immediately in front of the hearts. They are the sole afferent vessels of the intestinal walls. There are no such vessels in Megascolex cœruleus, their function is performed by the intestino-tegumentary vessels.

Ventro-tegumentary Vessels.—These are branches of the ventral vessel connecting it with the peripheral networks. There is a pair of these vessels in every segment except the first, in which there is a branch of that belonging to the 2nd segment on each side, and except in those segments in which the ventral vessel is joined by hearts, viz. Segments VI, VII, VIII, and IX, and in Segment X.

In Segments VI, VII, and VIII the place of ventro-tegumentary vessels is taken by vessels which come off from a bulbous dilatation, which is interposed between the heart proper and the ventral vessel. The limit of the heart proper is marked by a sphincter, and between this sphincter and the ventral vessel is the bulbous dilatation.

In Segment VIII, in addition to the ventro-tegumentary vessels belonging to that segment, there is a second pair of vessels arising from the bulbous dilatations which run backwards through Septum VIII-IX, and form the ventro-tegumentary vessels, or rather the vessels which correspond to them, of Segments IX and X.

Ordinarily these ventro-tegumentary vessels come off from the ventral vessel immediately in front of the septum which

bounds posteriorly the segment to which they belong, so that they lie in the posterior portion of their segment.

These ventro-tegumentary vessels supply not only the body-wall, but all the viscera excepting only the walls of the alimentary canal, and they and their branches almost always run strictly side by side with vessels belonging to the latero-longitudinal and subneural system; their finest branches (capillaries) are in every case continuous with the finest branches of this system—they are, in fact, the afferent vessels while the branches of the latero-longitudinal and subneural system are the efferent vessels of the tissues. So closely are these afferent and efferent vessels associated throughout the greater part of their course that I have again and again imagined that I was dealing with a single vessel, but when I knew what to expect, more careful examination always revealed two vessels lying side by side and branching at the same spots.

As a type of what occurs with regard to the majority of these ventro-tegumentary vessels we may take that of Segment XII. The vessel lies on the mesentery and runs towards the dorsal region : it sends outwards towards the body-wall a series of branches; the first of these supplies the region of the body-wall which lies ventrad of the inner row of setæ following this; then there are three branches going to the region of the body-wall which lies between the two rows of setæ, and near the first of these a branch to the nephridium of the next following segment (to the nephridium, that is to say, all of which except the funnel lies in the next following segment). Up to the point where the last of these branches is given off, the vessel is closely accompanied by a branch of the subneural vessel, but at this point the ventro-tegumentary vessel leaves for a short time the subneural-tegumentary branch and runs more closely along the body-wall, giving off a series of five or six small vessels in its course towards the dorsal region. The subdivisions of all these branches to the body-wall run backwards as well as forwards, so that the vessel is not distributed to its own segment only, but to the anterior portion of the next

following segment. There is, however, so far as I can see, no anastomosis between the branches of one ventro-tegumentary vessel and those of another.

In Segments VI, VII, and VIII each ventro-tegumentary vessel, very soon after its origin from the bulbous enlargement at the base of the heart, gives off a small branch which supplies the wall of the heart itself and the wall of the dorsal vessel; the next branch runs along the anterior surface of the septum which bounds posteriorly the segment to which it belongs, gives off some small branches, and then passes up towards the dorsal region of the posterior portion of the body-wall of the segment, giving off numerous branches, some of which run backwards and some forwards, while all supply the various layers of the body-wall. The ventro-tegumentary vessel itself runs forward in the segment and gives off a branch to the nephridium, and, lastly, supplies the posterior side of the septum which bounds the segment anteriorly, and, passing towards the dorsal region, supplies the body-wall of the anterior portion of the segment.

The ventro-tegumentary vessel, which originates in Segment VIII but passes backwards to supply Segments IX, X, and, to a certain extent, XI, is the largest of the whole series. It penetrates the Septum VIII-IX close alongside the latero-longitudinal vessel and runs backwards with this. It gives off a branch to the posterior side of Septum VIII-IX and the anterior region of the body-wall of IX, one of the subdivisions of which branch forms the afferent vessel of the nephridium of Segment IX, then a branch to the posterior portion of the body-wall of Segment IX, which will be seen from fig. 27 to pass just in front of the external aperture of the nephridium of Segment X, and close to this last branch another, which, after giving off a small branch to the wall of the heart of Segment IX, passes to the seminal capsule; its next branch supplies the nephridium of Segment X; its next branch, after giving off a vessel to the prostate, supplies the ventral region of the body-wall in the anterior portion of Segment X, and then, after giving off a branch which goes to the nephridium

of Segment XI and also to the ovary, this vessel supplies the dorsal region of the body-wall of Segment X.

The ventro-tegumentary vessel of Segment V calls for special remark. After leaving the ventral vessel it runs outwards and forwards along the body-wall towards the dorsal region. The first branch runs to the salivary glands, the second penetrates the muscular layers of the body-wall; the next two branches come off at almost exactly the same spot; the one supplies the nephridium of Segment V, the other runs forwards, and on its way supplies the nephridia of Segments IV and III. There are seven other branches, which all run forward and penetrate the body-wall. There are thus eight branches from each of these ventro-tegmentary vessels (those of Segment V), which run forwards in the body-wall of the anterior extremity.

The ventro-tegumentary vessels of Segments IV, III, and II are all small.

The ventral vessel comes to an end anteriorly in the region of the subœsophageal ganglion by giving off the ventro-tegumentary vessels of Segment II, each of which gives off three main branches, supplying, doubtless, the prostomial and peristomial regions, and of course Segment II.

Dorso-tegumentary Vessels.—These are branches of the dorsal vessel connecting it with the peripheral networks.

All the branches of the dorsal vessel anterior to the hearts, and one pair of those branches in each segment posterior to them, belong to this category.

In the most anterior portion of the dorsal vessel they arise from this slightly irregularly, i. e. asymmetrically.

In all other segments they arise regularly from the dorsal vessel immediately in front of the septum, which forms the anterior boundary of the segment in which they lie.

All these dorso-tegumentary vessels which arise behind the hearts have similar relations. Each runs boldly outwards, unattached to any other structure, and appearing always as though the blood in it was under considerable pressure, and at about the outer seta line it bifurcates; the two branches are really portions of the subneural system, and are coloured blue in

fig. 27. One branch—the "branche tegumentaire" of Jaquet[1] —runs on to the body, comes into the neighbourhood of the distal portion of the ventro-tegumentary vessel of the segment, and runs along parallel to this towards the dorsal median line; its branches run parallel to those of the ventro-tegumentary vessel, and their capillaries communicate. It is evident that, as the ventro-tegumentary vessel is the afferent vessel for these capillaries, this branch of the dorso-tegumentary vessel is the efferent vessel. The other branch (the "branche dorso-sous-nervien" of Jaquet) loops round and becomes directly continuous with the branch of the subneural vessel belonging to the segment; from about the outer seta line inwards it runs parallel to and close alongside of the proximal portion of the ventro-tegumentary vessel, and there are branches of this dorso-subneural vessel corresponding to each of the branches of this portion of the ventro-tegumentary vessel; there are, again, efferent vessels of the capillary networks in the body-wall and nephridia, supplied by the ventro-tegumentary vessel.

There is thus a loop or commissural vessel which is connected on the one hand with the dorsal vessel, and on the other with the subneural vessel, all the branches of which bring blood back from capillaries. Does this blood pass into the dorsal vessel or into the subneural vessel, or into both? I believe that the blood passes into the subneural vessel only, and that no blood enters the dorsal vessel by means of the dorso-tegumentary vessel. I have already discussed this question when speaking of Megascolex, and although we are now dealing with a very different genus, it is not, I think, on a priori grounds, likely that the dorso-tegumentary vessel would carry blood out of the dorsal vessel in the one case and into it in the other; moreover, in Moniligaster as in Megascolex, while there are valves which would mechanically prevent blood flowing into the dorso-intestinal vessels from the dorsal vessel, there are no such valves where the dorso-tegumentary vessels join the dorsal vessel. I have, however, observed in Moniligaster and some other worms a sphincter muscle in the wall of the

[1] 'Mitth. Zool. Stat. Neap.,' Bd. vi, 1885–6.

dorso-tegumentary vessel close to its origin. Now if it were the usual thing for blood to enter the dorsal vessel from the dorso-tegumentary vessels, there would, judging from analogy, be valves which, acting mechanically, would prevent blood taking the reverse direction during the powerful contraction of the dorsal vessel; if, on the other hand, the normal course is for the blood to pass out into these dorso-tegumentary vessels, the sphincter muscles on the latter would regulate the amount so passed out. I do not believe that any great quantity of blood flows through these vessels at all, but that what flow there is is an outward one, and one which would serve to increase the pressure in the peripheral capillaries, and could be varied in amount from time to time and regulated.[1]

[1] Benham thinks that the dorso-tegumentary vessels bring blood to the dorsal vessel. He is speaking of Lumbricus, but, as far as I can see, there is very little difference between Lumbricus and Moniligaster in the matter of the vascular system. The diagram (fig. 34), represents the state of things in an ordinary segment of Moniligaster. In this figure I have inserted various arrows to indicate the possible direction of the blood-flow. Now I think that there is no question as the correctness of these arrows ⋙——>, and I believe that these arrows ≫——> are also rightly placed; Benham considers these arrow >——> to be correct. I consider the question settled in Moniligaster by the valves; Benham thinks that his view is confirmed by the arrangement of valves in Lumbricus. Setting aside for a moment the question of valves, let us follow out his view. He says, that in all these places blood is flowing out from the subneural vessel; very well, where does it flow into the subneural? The subneural is, as far as I can make out, always a part of a system of vessels of which the latero-longitudinals form another part; now this system is known to be connected in Moniligaster and Lumbricus with the dorsal vessel (or a pair of hearts). It is from the dorsal vessel (or hearts), then, that the subneural must get its blood, which means that blood must flow, according to Benham's theory, from the dorsal vessel into not only the subneural but into the whole system, including the latero-longitudinals; but branches of these latero-longitudinals evidently play an opposite rôle to the branches of the ventro-tegumentary vessels in the anterior part of the body, and if the latero-longitudinal vessels serve as arteries, the ventro-tegumentary vessels must serve as veins, and carry blood into the ventral vessel (in the anterior region of the body). I have already given my reasons for believing that this is not the case in Megascolex (l. c., p. 77), and I think that they hold good, mutatis mutandis,

Latero-longitudinal and Subneural System.—Having already spoken of the main vessels of this system, and made various references to their branches and detailed the distribution of the ventro-tegumentary vessels, which run for the most part strictly parallel to the branches of this system, it is not necessary to do more than refer the reader to fig. 27, where this system is shown throughout in blue.

Course of the Blood.

I have found it convenient to refer to the course taken by the blood in describing the anatomy of the vascular system, and I have, in writing of Megascolex cœruleus, dealt at length with certain general problems relating to the blood-flow in earthworms (see also below, p. 42), so that I need only summarise here the chief facts with regard to Moniligaster grandis.

The blood flows forwards in the dorsal vessel, and while a little passes on in the anterior portion of the dorsal vessel, most of it is forced down into the ventral vessel by means of the hearts (chiefly the three anterior pairs) and is distributed by the ventro-tegumentary vessels on the one hand, to peripheral capillaries, and by the ventro-intestinal vessels on the other hand, to the intestinal capillaries.

The peripheral capillaries in the region of the body behind the hearts are also supplied, to an extent which probably varies from time to time and is, I expect, never very great, from the dorsal vessel by means of the dorso-tegumentary vessels.

The blood sent to peripheral capillaries is returned by the latero-longitudinal and subneural system to the most posterior pair of hearts, and the blood sent to the intestinal walls is returned by the dorso-intestinal vessels to the dorsal vessel.

for Lumbricus. Upon my premises I do not think that the logical outcome of Benham's view is tenable.

But, apart from all this, I have investigated the arrangement of valves connected with these vessels in Lumbricus, and I think that it resembles that which obtains in Moniligaster.

Nephridia.

There is in Moniligaster grandis a pair of large nephridia in each segment except Segments I and II and (at any rate in the worm from which I cut sections of the anal end of the body) the two most posterior segments.

The nephridium consists of (1) a nephrostome or funnel which, with a small portion of the duct, is præseptal, (2) the nephrostomial duct passing from this to (3) the glandular lobe, (4) the vesicle duct leading to (5) the large vesicle, and (6) the terminal duct leading to the nephridiopore. Regions 2—6 are post-septal.

The general relations of these regions are shown in fig. 42. On the outside of the greater part of the nephridium there is a layer of connective tissue (fibrous, not vesicular), and outside this, again, a layer of cœlomic epithelium cells.[1] There is a continuous lumen passing from the nephrostome to the nephridiopore which is intra-cellular, at any rate as far as the entrance to the vesicle, and possibly even in the vesicle and terminal duct.

The lumen consists of the following regions :—("*St. a*") A narrow ciliated tube leading from the nephrostome to the glandular lobe; here it communicates with ("*ab*") a branching system of ductules, the cells pierced by which lie on the outside of the first third of the glandular lobe; these branching ductules collect into a narrow duct ("*bc*" and "*cd*"), which passes on to the apex of the glandular lobe and returns upon itself and passes right back to the first bend of the glandular lobe. Where there are two portions of this narrow duct running side by side (as there are in the distal two thirds of the glandular lobe), there are transverse ducts every here and there placing one of these limbs of the narrow duct in communication with the other (fully shown in the figure in a little

[1] These cells, as may be proved by the careful use of silver nitrate, occur on the wall of the vesicle, as well as elsewhere.

piece only of the spirally-twisted portion of the glandular lobe, diagrammatically shown in the apical position). Where the narrow tube ends (*d*) what may be called the middle tube commences; this ("*de*," "*ef*," and "*fg*") runs back along the whole length of the glandular lobe to the apex, and then returns upon itself and passes on to the proximal extremity of the glandular lobe (*g*), close to the spot where the latter was joined by the nephrostomial duct. The middle tube is followed by the wide tube (the vesicle duct, marked "*gh*") which enters the vesicle (at the point marked *h*). The shape of the vesicle is shown in the figure; there is a sphincter muscle (*j*) at the spot where the terminal duct is given off. The terminal duct is a wide duct, and is much longer in some of the nephridia (e. g. those of Segment XI) than in others.

The nephrostome is very like that of Lumbricus. I have studied a very large number of these organs and have counted between forty and fifty marginal cells, and have satisfied myself as to the existence of one or perhaps two central cells (in fig. 42 I have drawn one nucleus of such a cell, but in one preparation [fig. 43] at any rate there were two similar nuclei side by side). I have been unable to ascertain anything clearly with regard to "gutter" cells.

The nephrostomial duct penetrates the septum at a spot somewhat removed from the body-wall and opposite the inner seta rows. The nephrostome is about $\frac{1}{300}$ inch across at the widest part.

The nephrostomial duct has very thin walls, richly ciliated (I do not think that the cilia are arranged in spiral lines, there is no appearance of such an arrangement) and covered with connective tissue in which there is a little pigment, rendering the duct rather easy to follow.

In the branching system of ductules the lumen is always very irregular; it can be well seen in quite fresh preparations, the finer ramifications show only when distended with fluid. Fig. 46 accurately represents the appearance obtained by focussing just below the surface of a portion of this region of the glandular lobe, but I have seen in preparations treated

with a chromo-osmo-acetic acid mixture much finer ramifications which terminate in the periphery of cells. The limit between one cell and another does not show clearly, as it does in the case of similar cells in Hirudo.

The walls of the large ductules of this system are here and there set with cilia arranged very irregularly, and there are also numerous undulating structures composed of bundles of long cilia-like filaments running along, or very obliquely across, the lumen (fig. 45). At each end the filaments of the bundle are gathered together and attached to the wall of the ductule. The bundles vary in length from about $\frac{1}{200}$ inch to $\frac{1}{1000}$ inch, and each bundle consists of some ten or twelve filaments. When the movement is rapid the bundle undulates as a whole, the wave always starting from one end—the end nearest the nephrostome—but as the movement becomes slacker it constantly happens that the waves start at slightly different moments in the individual filaments, with the result that they separate from one another; in fact, a wave of separation passes along the bundle. Except for the fact that these filaments are attached at both ends, they are remarkably like the tufts of fine vibratile cilia which constitute the so-called "flame" of the excretory canals of the Platodes. I have made a very careful study of these structures, and am quite convinced of the accuracy of the above statements. They are quite clear in some of my chromo-osmo-acetic acid preparations, and on one occasion I watched them in a fresh preparation on and off for nine hours as the movement became gradually slower and slower.

The walls of the narrow duct are very like those of the narrow duct of Lumbricus in structure. I have never been able to quite satisfy myself that the branching tubules collect into one limb of the narrow duct only, as shown in fig. 42 at *b*, but I think that they do, and that the transverse tubules joining the two limbs of the narrow duct are secondary formations. I have not found cilia in any part of this narrow tube. The walls of the middle tube are much thicker, and they present a striation similar to that which I described as existing

in many of the nephridial cells of Hirudo. It is not ciliated in any part of its course. It frequently loops back upon itself; one such loop only is shown in fig. 42. The lumen presents a somewhat irregular contour.

The cells of the wide tube are similar to those of the middle tube, but the contour of the lumen is more regular. The wall of the vesicle is not lined inside by any layer of visible cells, but sections show scattered nuclei on the inner wall, and I think that the lumen must be intracellular, the cells being very much flattened out. There is a well-developed muscular layer which consists of an inner set of longitudinally placed fibres, and an outer set of more or less obliquely placed circular fibres. Outside the muscle is a little connective tissue, and outside all a layer of pavement (cœlomic) epithelium cells; these are very delicate, and, owing to the contraction of the muscle, somewhat difficult to demonstrate, but in a fortunate silver preparation they are very clear indeed. The vesicle is a tube closed at either end, and has a short prolongation on one side leading to the terminal duct. At the junction there is a well-developed sphincter, and the lining epithelium is ciliated all round the aperture. The terminal duct has very thin walls; these are like those of the vesicle, except that there is no muscle. The connective-tissue layer is very thin, but very strong, and appears structureless.

I have already spoken of the very elaborate vascular supply of the nephridia.

Nervous System.

The cerebral ganglion lies as usual far forward on the dorsal wall of the pharynx. It is a single, somewhat square-shaped lobe (fig. 27). Arising from its anterior outer corners are the œsophageal commissures. These join together to form the subœsophageal ganglion, whence arise the ventral cords, which are united at intervals by ganglia. These cords are firmly bound up together, by a sheath composed of muscular and connective tissue, into a single cord; but as nerves they are really as separate and distinct from one another in the

interganglionic regions as are the nerve cords of a leech. The ganglia, however, spread along the cords so that the interganglionic regions become very short, and two or three other post-oral ganglia fuse with the subœsophageal ganglion itself. The ganglion lies in the anterior region of a segment.

A nerve arises on each side from the anterior edge of the cerebral ganglion, the branches of which clearly supply the prostomium.

Five nerves arise on each side from the inner surface of the commissure, and pass on to the pharyngeal wall to form a stomato-gastric system. I find no nerve ring on the pharyngeal wall. Ordinarily three nerves arise on each side from each ganglion. One of these arises from the anterior portion of the ganglion, and this passes at once into the septum (see this branch, of the right hand side, in Segment VII in fig. 27. The septa are supposed to have been dissected entirely away in Segments IX and X). In the case of the thickened septa this nerve can be very clearly seen running in between the muscular layers of the septum; it passes into the body-wall, and runs round towards the dorsal region, behind the intersegmental groove.

The other two nerves arise very near together from the middle region of the ganglion. They run outwards near the inner surface of the body-wall until they reach the inner seta row. Here they penetrate the body-wall, and run round towards the dorsal region between the muscle and the epidermis. The more posterior one of the two gives off a large branch soon after penetrating the body-wall, which also runs round towards the dorsal region.

These three nerves may be called the first, second, and third nerves of the segment respectively.

The first nerve gives off a small branch, which bifurcates and is supplied to the septum.

The second and third nerves each give off a small branch before arriving at the inner seta line; these branches join and supply, I believe, the viscera of the segment (except the alimentary canal).

The third nerve also gives off another branch before it arrives at the inner seta line, which runs backwards and joins the branch of the first nerve of the next following segment.

The three nerves of the 1st segment which really arise from the subœsophageal ganglion appear to come off from the commissure.

From about Segment xx onwards the second and third nerves arise so close together as to be indistinguishable one from the other, but the microscope shows distinct bands of fibres, and they separate after penetrating the body-wall.

The histology of the ventral cord is dealt with in figs. 47, 48. The cord is covered throughout by flattened cœlomic epithelium cells. Under these is a layer of connective tissue in which occur large oval nuclei. Then follows a very thick sheath of almost hyaline substance in which are embedded the muscle-fibres; this shrinks away from the outer connective-tissue sheath in preserved specimens, as shown in the drawings; a few scattered histological elements occur in it.

The muscle is present in enormous quantity as compared with other worms. It consists of longitudinally running cells placed either singly or in bundles. At the origins of the nerves these muscle cells run outwards to form a sheath to the nerve (fig. 48).

With regard to the nerve tissue proper, there is a single giant-fibre only; in the inter-ganglionic regions, the two nerve-cords are quite distinct from one another and from the giant-fibre; the inner and dorsal portion alone of each cord is occupied by longitudinally running nerve-fibres arranged more or less definitely in bundles; in the ganglia the two cords and the giant-fibre all form part of the same mass, the nerve-fibres retain here a similar position while the ganglion cells lie on the outer and ventral sides.

Both the sections figured run slightly obliquely across the cord, which accounts for the facts that in fig. 47 one cord is slightly larger than the other, and that in fig. 48 the origin of a nerve is seen on one side only.

GENERATIVE SYSTEM.

This consists of a pair of testes, each testis lying in a sperm-sac, a portion of the wall of which forms the "ciliated rosette," and is continued as sperm-duct to open into the atrium on each side, the prostate glands, a pair of ovaries, a pair of oviducts formed by a modification of the septal wall, a pair of ovisacs, and a single pair of spermathecæ provided with long ducts which present special enlargements, copulatory pouches, close to their external apertures.

The testes belong to Segment IX, the ovaries to Segment XI, the spermathecæ to Segment VIII.

Sperm-sacs, Testes, Ciliated Rosettes, Sperm-ducts, Atria, and Prostates.—The sperm-sacs are suspended in Septum IX-X. Each appears in the adult to pierce the septum so that half lies in one segment and half in the other, while the septum is attached all round the equator, so to speak, of the sac. The sac can be pushed forwards or backwards, carrying the septum along its attachment with it, and when this is done, the septum, owing to its contractility, shrinks behind or in front of them so that they appear then to lie wholly in one segment or the other. Sections of a young worm in which the sperm-sacs were just visible to the naked eye show the sperm-sac lying in front of, although in contact with, Septum IX-X. The sperm-sac is oval in shape; it contains the testis, and in the adult, developing spermatozoa, while a portion of its wall forms the "ciliated rosette." The cavity is traversed by trabeculæ which consist of blood-vessels with a minute amount of connective tissue and muscle.

The testis is attached to the inner wall of the sac on the ventral side, in front of the "ciliated rosette." It is a small, white, flattened body, divided up into lobes at its free edge, and resembles in structure the testis of other earthworms.

The sperm-duct joins the sperm-sac just behind the testis, but still in front of the equatorial attachment of the septum—i. e. in Segment IX—and its wall spreads out so as to become, I think, the walls of the sac. The epithelium lining the sperm-

sac is thick all round the entrance of the sperm-duct, and ciliated; it forms, in fact, the "ciliated rosette," which does not stand out freely into the cavity of the sac at all: indeed, the ciliated epithelium is directly continuous with the rest of the epithelium of the sperm-sac. The "ciliated rosette" does not even present any convolutions of its surface.

The sperm-duct is much convoluted, and the whole is supported and its convolutions bound together by a special development of the mesentery, which in other segments supports the nephridia. A mass of convolutions lies anterior to Septum ix-x, the duct then penetrates the septum, and another mass lies posterior to the septum; finally the duct runs down and enters the prostate close to the body-wall, and at its inner (median) side. The sperm-duct is enormously long; I have completely unravelled it under a dissecting microscope, and found that when straightened out, without stretching, it measures as much as 9½ inches.

I cannot suggest what may be the use of this great length. Its walls are ciliated and not glandular, and the spermatozoa are not, I believe, built up into spermatophores.

The wall consists of a layer of slightly flattened cells, ciliated upon apparently a portion of their surface only, while outside is a thick layer of connective tissue. There is no muscle in the wall (figs. 53, 54).

The sperm-duct opens into the atrium. The shape of the atrium varies according as the papilla bearing the male pore is protruded or withdrawn, and as the muscles of its own walls are contracted or relaxed. When the papilla is protruded the atrium is a mere tube; when the papilla is withdrawn, if the muscles in the atrial wall are relaxed, the cavity is approximately spherical; but if the muscles are contracted the epithelial lining becomes much plicated and the cavity quite irregular.

The atrial epithelium consists of two kinds of cells—non-glandular columnar cells and greatly elongated gland-cells, which dip down a great distance below the epithelial layer, and are arranged in groups. Each, however, sends its duct up

to take its place among the columnar cells. These gland-cells do not occur near the external aperture; the glandular mass formed by them constitutes the "prostate;" a layer of muscle, the fibres of which run in various directions, overlies the epithelial layer; outside this comes the thick layer formed by the deep-lying glandular portions of the prostatic cells; outside this is another layer of muscle, and outside this the ordinary layer of cœlomic epithelium. The nuclei of these epithelium-cells can be seen with difficulty in sections, but the presence of the cells themselves may be very clearly demonstrated by the use of silver nitrate.

The sperm-duct penetrates the prostate, and then opens into the atrium at the point furthest from the male pores (fig. 55).

Ovaries, Oviducts, and Ovisacs.—The ovaries lie in Segment XI, or rather in that closed portion of the segment which contains also the nephridium; they are not therefore exposed in an ordinary dorsal dissection. When the septum is cut so as to expose them, they are seen as large, brilliantly white, frill-like organs; they really lie above and at the side of the œsophagus, and not near the ventral wall. They are as much as $\frac{1}{2}$ inch long and $\frac{1}{8}$ inch deep. Each is really a very closely-set zigzag, the free edge of which is slightly lobed and thicker than the attached edge owing to the greater development of the ova which are set free from the free edge (figs. 50 and 57).

The oviduct is merely a modification of a portion of Septum XI-XII. There is nothing standing out freely into the segment. The epithelium is thickened and thrown into folds and ciliated, and as the wall is very thin in the intersegmental region, there is a very short little duct running to the exterior; the aperture, as mentioned above, is strictly intersegmental. The ovisacs are diverticula of that portion of Septum XI-XII which forms part of the wall of the sac containing the ovaries and nephridia of Segment XI; they, and indeed the whole sac, become packed with ova; the pair of ovisacs and this portion of Segment XI thus packed are shown of natural size in fig. 51. A young ovisac just developing is shown in fig. 59. The wall becomes thick and very vascular, and when packed with ova there is an

exceedingly rich network of capillaries forming a perfect network throughout the lumen; very little, if any, connective tissue accompanies these capillaries. The ova lie in the meshes, and the whole thing becomes like an exceedingly vascular solid gland; the ova, however, remain perfectly free and imbibe nutriment, and attain three or four times the size they were when they entered the sac. A ripe ovum is about $\frac{3}{1000}$ inch in diameter.

Spermathecæ, Spermathecal Ducts, and Copulatory Pouches.—The spermathecæ are pear-shaped, and the duct is continued from the thin end. They lie attached by mesentery to the posterior face of Septum VII-VIII at the level of the œsophagus. The duct held by the mesentery coils a good deal, and then penetrates the septum and runs along for a considerable distance embedded in the muscle of the septum. It never actually passes through into Segment VII. It opens into a very small oval pouch, which is itself embedded in the body-wall and opens to the exterior. The pouch must serve as a copulatory pouch, and may be so styled.

The spermathecal wall presents a muscular layer immediately under the cœlomic epithelium, and below this comes the spermathecal epithelium. Near the opening of the duct and for some little distance inwards the epithelium is composed of small columnar cells, but the rest of the epithelium is glandular. All the cells appear to be gland-cells, but they are long narrow cells; the epithelium in this glandular region is about three times as thick as elsewhere. The epithelium of the duct is composed of very small cells, outside this is a muscular layer. The epithelium of the copulatory pouch is composed of rather larger cells, but they are still small and not glandular, and it must be remembered that a papilla can be protruded here, and when this is done the pouch must become a tube as is the case with the atrium.

I have found in the spermatheca masses of spermatozoa and an albuminous-looking mass, secreted doubtless by the glandular cells, as there is generally a mass of it up at that end of the sac.

The Vascular System in some other Species of Moniligaster.

The two main variations from the arrangement of this system in M. grandis which obtain among my species are:

1. A supra-intestinal vessel may be present.
2. The latero-longitudinal and subneural system may communicate with two pairs of hearts instead of only one.

In M. pellucida there is a supra-intestinal vessel (fig. 30). This means that the intestinal veins of certain segments—in this case Segments x—xviii—instead of opening into the dorsal vessel by means of dorso-intestinal vessels, collect into a special trunk—the supra-intestinal—which, after receiving all the blood from the latero-longitudinal and subneural system, communicates with the most posterior pair of hearts; the dorsal vessel has no connection with these, they are therefore intestinal hearts.[1]

The supra-intestinal vessel is practically a specialisation of the latero-longitudinal and subneural system.

In M. sapphirinaoïdes, M. ophidioïdes, and M. robusta the latero-longitudinal and subneural system communicates with hearts as in M. grandis, but in addition to vessels passing up to the hearts of Segment ix, as in the latter species, there is a similar pair opening into the hearts of Segment viii. This entails no other variations.

In fig. 29 I have shown the way in which the subneural trunk communicates with the latero-longitudinals. There is always asymmetry in this region, the connecting trunk being always larger on the right hand side than on the left. The communication here is better developed than in M. grandis, but in neither case does it seem perhaps to be a very ample way of providing for the return of all the blood from the peripheral capillaries in the posterior region of the body to the dorsal vessel or hearts, but it must suffice for the purpose, and it

[1] Cf. Bourne on Megascolex cœruleus, in 'Quart. Journ. Micr. Sci.,' vol. xxxii, p. 64, footnote.

must be borne in mind that the flow is here a continuous one while in the arteries it is intermittent.

The arrangement of the vessels in a segment of M. ophidioïdes shown in fig. 28 emphasises my view as to the direction of the blood flow, such as it is, in the dorso-tegumentary vessels. The dorso-intestinal vessels on the gizzard wall have a characteristic arrangement which is here shown.

Generalisations with regard to the Vascular System in Earthworms.

I am now in a position to offer some wider generalisations with regard to this system than I was when writing on Megascolex cœruleus, but, considering the large number of genera known, our information on the subject is still very scanty. If the anatomical relations of their afferent and efferent vessels be taken into account, we may conveniently distinguish two sets of capillary "networks" and term them respectively peripheral and intestinal networks. To the former category belong all capillaries in the body-wall, septa, nerve-cord, nephridia, and, indeed, all the viscera except the intestine. To the latter category belong the capillaries in the intestinal wall; and here we must distinguish in some worms between those in the anterior region and those in the region behind the gizzard, those in the anterior region having in some worms relations similar to those of peripheral networks.

It is, I think, desirable to use the terms artery and vein for the vessels which have relations with the capillary networks. We can recognise:

1. Arteries which carry blood from the main trunks towards capillary networks; these arise from the main trunks and then repeatedly subdivide.

2. Veins which carry blood from capillary networks to main trunks; these are formed by the repeated junction of smaller vessels, and finally open as single large vessels into a main trunk.

3. Veins which, like the vertebrate portal vein, carry blood from one capillary network to another. These are vessels or

networks of vessels, the branches of which all repeatedly subdivide until they become capillaries, some of which, i. e. those in one particular region of the body, are continuous with the capillaries formed by an artery, and others with those formed by an ordinary vein.

I shall speak of these last-mentioned veins collectively as a portal system.[1]

The most important distinction which I find between the vascular system of one worm and that of another lies in the presence or absence of a "portal system." Where a portal system is present there are no intestinal arteries; the blood is brought to the capillaries of the intestine from the peripheral capillaries by means of the portal system.

Where there is no portal system the intestine receives intestinal arteries (ventro-intestinal vessels), while the blood in the peripheral networks is carried by ordinary veins (latero-longitudinal and subneural vessels) direct to the main trunks (dorsal vessel, supra-intestinal vessel, or hearts).

There is no portal system in Moniligaster or Lumbricus, while on the other hand I have observed such a system in all the Perichætidæ which I have examined, in Perionyx and Acanthodrilus, and from facts recorded by Perrier and Benham, I have no doubt but that such is present in Urochæta, Pontodrilus, Microchæta, Rhinodrilus, Plutellus, Digaster, and Titanus.

The character which seems to me to come next to the presence or absence of a portal system in order of importance is the presence or absence of a subneural trunk.

Where a subneural is present in addition to a portal system, as in Urochæta and Perichæta (sensu restrictu) it appears to take some of the blood more directly into a main trunk (a conclusion to which I am led by a study of Perichæta).

Where a subneural is present without a portal system it

[1] As the term "portal" is now in general use to designate veins other than that to which it was originally applied, there seems to be no objection to its use for all vessels having similar relationships with regard to capillary networks.

forms the main trunk of the venous system in the posterior region of the body, while the latero-longitudinals form the main trunks in the anterior region, and they join together to open into the dorsal vessel or a pair or pairs of hearts.

Megascolides appears to have no portal system, because, according to Spencer, the latero-longitudinals open into the dorsal vessel; but no subneural is present, and no mention is made of ventro-intestinal vessels; so that unless the blood carried outwards by ventro-tegumentary vessels is returned to the dorsal vessel by the dorso-tegumentary vessels, and blood is supplied to the intestinal wall by dorso-intestinal vessels and returned—where and how we do not know—I am at a loss to explain Spencer's account. But I am not prepared to base any arguments upon it, as one might imagine from the account that there was a perpetual supply of blood to the various capillaries which never returned thence.

Other variations in the vascular system are of apparently less importance, e. g. a supra-intestinal vessel is present in some species of a genus and absent in others.

With regard to the course of the blood, I have little to add to what I have already said with regard to Megascolex cœruleus and Moniligaster grandis. These two types cover, with slight variations, all cases which I expect exist, except a case where there is no portal system and no subneural vessel; in such a case—and, as Spencer's description stands, Megascolides presents this arrangement—the dorso-tegumentary vessels may be the veins of the peripheral capillaries. I have again and again returned to the course taken by the blood in these vessels. I cannot help thinking that primitively they are efferent vessels, and that both they and the dorso-intestinal vessels bring blood to the dorsal vessel. In this case they can only have, in worms otherwise well provided with a venous system, the function suggested above for M. grandis of regulating the pressure in the peripheral capillaries, and have practically no flow in them in one direction or the other. In this case it would not be surprising, in cases where there is no portal system and no subneural vessel or other main venous

trunk, to find them acting as veins. This theory is borne out by observations on the development of a large Perichæte. I do not find any stage in which commissural vessels run in each segment from the dorsal vessel to the ventral; the hearts develop as such vessels, but in all the segments, those containing the hearts as well as the others, a pair of dorso-tegumentary and a pair of ventro-tegumentary vessels develop and communicate only through capillaries, so that at this stage the ventro-tegumentary vessels are the arteries of the peripheral tissues, and the dorso-tegumentary vessels the veins. This is a worm which, like all Perichætæ, subsequently develops intestino-tegumentary vessels.

Notes on the Clitellum and Generative Organs.

Clitellum.—Beddard (13) has figured the structure of the clitellum and insists upon its being composed of "a single layer of cells," by which I presume he means that none of the cells dip down into the body-wall further than others, but they do so to a certain extent in his figure, and they do so to a great extent in all the clitella which I have examined, and I expect that the clitellum of his specimen of M. bahamensis was not fully developed.

Even in the most fully-developed clitella which I have examined, a number of the cells remain unglandular between those which have become glandular, a state of things which does not appear to occur in other earthworms.

Generative Organs.—The resemblance of these organs to those of various lower Oligochæta is, as has been fully pointed out, very striking. My observations all tend to confirm the resemblance.

The ciliation of the sperm-ducts is a very striking feature.

The testes undoubtedly belong to Segment IX. I may anticipate my observations on the development of the genus by stating that these organs develop as proliferations of the cœlomic epithelium of the anterior face of Septum IX-X, and the ovaries as precisely similar structures on the posterior

face of Septum x-xi, while no rudimentary genital organs form in any other segment. The "ciliated rosette" develops, I believe, from the epithelium of this septum just ventrad of the testis, and afterwards, together with some of the muscles of the septum, grows round to enclose the testis and form the sperm-sac. The development of the sperm-duct I have not yet been able to make out. The wide mouth of the oviduct is in the adult nothing but a specialised portion of the septal wall. So that there seems to be in Moniligaster no connection between genital ducts and nephridia.

With regard to the relation of prostate to atrium I agree entirely with Benham (14), but I find that each gland-cell in the prostate opens by its own duct into the atrium, that it is, in fact, merely an enlarged cell of the atrial epithelium, so that I do not see why we should use the term "multicellular gland." The cœlomic epithelium is always to be found outside the other structures, in the form of pavement cells easily demonstrated by the use of silver nitrate.

Systematic Account of the Genus Moniligaster.

Before describing any other species[1] I shall discuss the value of the various characters for systematic purposes, taking account of my own observations only.

Colour has a certain value; there are groups of species with pigment in the body-wall (figs. 6—10) and groups with little or no pigment (figs. 3, 4), but the exact colouring varies much in some cases within the species (figs. 8—10).

Size has some importance as there is great variation, but the condition of the worm when measured must be estimated (see above, M. grandis—size, p. 307), and the specimen must be

[1] Out of the thirteen species described below, I place three (M. grandis, M. naduvatamensis, and M. nilamburensis) in one group and call it in the following account the M. grandis group; three (M. ophidioïdes, M. robusta, and M. sapphirinaoïdes) in another group and call this the ophidioid group; two (M. pellucida and M. uniqua) in another group and call this the pellucid group; the other species I do not group together in any way.

adult as shown by the generative organs; even then there is a variation of at least 25 per cent. of the total length between adult individuals of the same species. This variation does not depend upon age, there are long individuals and short individuals as in the human species. I have proved this by observations taken at the time of hatching; at this time and indeed long before, growth by the addition of new segments has ceased while there is considerable variation in the number of segments—and the adult length depends, given an equal amount of contraction, solely upon the number of segments. The well-known phenomenon of regeneration of tail segments must be mentioned in this connection; where the original tail has been injured the number of new segments which may form seems to be about the same as the number lost, as in any species the total number varies only to the extent of the usual percentage, whether the individuals have regenerated tails or not. I give a tabular statement for M. sapphirinaoïdes. The specimens were part of the same collection, from the same spot, and it was from this same collection that the nine specimens described below as varieties of this species were taken. The specimens in both cases were taken at random.

Specimen.	Length.	Number of Original Segments.	Number of Re-generated Segments.	Total.	Remarks.
1	170 mm.	140	15	155	
2	155 „	168	—	168	
3	180 „	148	12	160	
4	117 „	91	26	117	Abnormal.
5	220 „	143	56	199	
6	160 „	172	—	172	
7	150 „	170	—	170	
8	170 „	133	44	177	
9	150 „	140	—	140	
10	115 „	115	11 + 6	132	Twice injured.
11	95 „	146	10	156	Apparently still growing.
12	190 „	163	36	199	
13	95 „	84	40	124	Still growing.
14	112 „	109	6	115	Still growing.
15	120 „	160	—	160	
16	140 „	140	24	164	
17	160 „	139	37	176	
18	120 „	164	—	164	
19	160 „	164	—	164	
20	145 „	157	—	157	
21	95 „	150	—	150	
22	115 „	172	—	172	

We get an average number of segments in the specimens which had not been injured of 162, and in those which had grown new tails of 156, or, omitting Nos. 13 and 14 which were still growing, and No. 10 which had been twice injured, and No. 4 which was abnormal, the half segments on one side not always corresponding with the halves on the other side, we get an average of 161 segments in an injured worm to correspond with the average of 162 segments in an uninjured one.

Segments.—I have spoken above of their number. Some importance attaches to the variation in size of the anterior segments (compare figs. 1 and 6 with figs. 5 and 12). Annulation of the segments, which depends upon a particular arrangement of the circular muscles, is characteristic of groups of species.

Prostomium.—This presents no easily recognisable variation in the group (see M. grandis—prostomium, p. 309).

Setæ.—The length varies in the group (my species) from

0·24 mm. to 0·63 mm., but in variable species like M. sapphirinaoïdes it varies in different individuals from 0·375 mm. to 0·625 mm., so that I have judged of the normal size for the species after examining several individuals only. There is no appreciable variation in the size of different setæ (full grown and unbroken) from any one individual.

The presence or absence of all or one couple from Segment II is a good specific character, but I have found them present in individuals of a species where they are as a rule absent.

The two setæ of a couple are always very close together.

The position of the rows of couples, i. e. the extent of the dorsal, lateral, and ventral gaps, is a very good specific character, and only fails, to my knowledge, in the case of what I consider to be hybrids between M. ophidioïdes, M. robusta, and M. sapphirinaoïdes, and between M. uniqua and M. pellucida. The position of the seta rows is only quite obvious (without mounting) in most species behind about Segment XIII, but from that point onwards the relative distance of the rows to one another does not vary in the individual.

Occasionally in a species the distance between the two setæ of a couple is greater than usual. My only instance of this is M. nilamburensis.

Clitellum.—This, owing to its transient nature, would not in any case be a good character (it does not show externally for more than a month or two in the year, but I doubt very much whether, having been once developed, it would ever become unrecognisable in sections; I have never found it so). So far as my observations go it always develops, and that upon Segments X—XIII, strictly confined to those segments, never complete ventrally (see M. grandis—clitellum), and never obscuring, or developing over, the intersegmental grooves. All the egg-capsules of Moniligasters I know (I have never found those of M. grandis[1]) are perfectly neatly formed and very globular.

[1] The small worm which so often occurs crawling in the mucus on M. grandis, is not, as I at first thought, the young of this animal; nor is it a Moniligaster at all.

In a M. sapphirinaoïdes where the clitellum is well developed, the worm, when suddenly killed, makes this region of the body very globular by means of certain muscles running from the dorsal to the ventral part of the segment on each side, and it no doubt assumes this shape when forming the egg-capsule, and allows the semi-fluid secretion to set before resuming its ordinary shape and crawling out.

Dorsal pores are never, to my knowledge, present.

Nephridiopores are usually placed on the very anterior margin of the segment in the direction of the outer seta rows, but the more dorsal position of the pores of Segments III—IX, and occasionally others, forms a good specific character. It serves, for instance, to distinguish between M. grandis and M. naduvatamensis, but in the "ophidioid" group (see below) is liable to variation.

Genital Apertures.—These always lie between the same segments, viz. VII-VIII, X-XI, XI-XII. There is a slight specific variation as to their relative distance from the median line, but they always lie somewhere between the direction of the outer and inner seta rows or precisely in the direction of one of those rows. With regard to their character, I can only say that in the M. grandis group and in the pellucid group papillæ commonly protrude from the male pores when killed, while in the ophidioid group they do not.

Body-wall.—This is thickened at the sides in the ophidioid group, enabling them to move very rapidly in a serpentine manner.

Septa.—The only septa which thicken are V-VI to VIII-IX, and these vary in different species in the extent to which they are thickened, the most anterior being in some cases hardly any thicker than the majority of septa in the body. The peculiar arrangement of some of the septa such as is described in M. grandis obtains to a greater or less extent in all species. One variation deserves special notice: in some cases, as in M. grandis, the arrangement of Septum X-XI is such as to completely shut off the ovaries and oviducts and the apertures of the ovisacs from the rest of the cavity of the segment;

this modification obtains only when the worm is fully adult; in other species even in the adult this modification does not obtain. I express these two conditions by saying "ovaries enclosed" or "ovaries free" as the case may be.

Muscles.—The longitudinal muscles have in some and not in other species the "feathered" arrangement.

Setal muscle-bands are present or absent according as the setæ project or not into the cœlom.

Alimentary Canal.—The number of the gizzards and the particular segments in which they occur, although subject to a considerable amount of individual variation, is to a certain extent a good specific character. It is not difficult by examining a number of individuals to determine the number of gizzards normal for the species, and it is possible, by examining a still larger number, in some cases to fix upon a normal position. It is very common to find a slight gizzard development in front of or behind the normal gizzards, and sometimes these additional gizzards are as large as the others. The gizzards which do develop are always in contiguous segments. There are rarely if ever more than one or two gizzards in excess of the normal number. The variation in position depends of course for one thing upon the number of gizzards developed, but given the normal number the position may still vary, especially in some species, by two or even three segments. It is evident that the œsophageal wall in the gizzard neighbourhood can very easily produce these muscular developments, and the variation in position is fully accounted for by the fact that the mesenteron is not primarily metamerically segmented, and that the portion of the gut bounded by any particular septa is not necessarily homogenous with the portion bounded by the homogenous septa, in another individual.

A typhlosole is never present.

Vascular System.—This presents slight individual variations only, but certain well-marked specific variations, some of which I describe elsewhere in this paper.

Nephridia.—I have not specially studied the variations in the structure of the nephridium; so far as my observations

go, it is always built upon the same general type as in M. grandis.

Nerve-cord.—This presents no marked variations.

Generative Organs.—It is with regard to these organs that the greatest variations are usually looked for, but there is in this genus, so far as it is known to me, the most striking anatomical, and indeed histological, uniformity in this matter. The testes may vary in the position of their attachment to the wall of the sperm-sac. The inner wall of the prostate may or may not present a layer of muscle between the gland-cells and the cœlomic epithelium; in the former case these organs present on opening the worm a shining appearance, and in the latter their glandular nature is very apparent. I express the latter condition by saying "prostates glandular in appearance." I have not examined them all histologically, and there may be in some species a few muscle-fibres present, even when I have called them "glandular;" but anyone who has compared the "glandular" with the "non-glandular" appearance cannot fail to distinguish between them, and I have never found individual variation in the matter.

The precise point of penetration of the sperm-duct into the prostate varies in different species. The prostates vary in shape to a limited extent in different species, but they also vary according as the glands are full or empty of secretion.

The spermathecæ and sperm-sacs vary in shape in different species, but they also vary according as they are full or empty, a pyriform spermatheca becomes almost globular when quite full, and an oval sperm-sac becomes to a slight extent broader along its shortest axes.

The most valuable character is to be found in the copulatory pouch; this is in some species small and completely embedded in the body-wall, and at first sight would be overlooked; in others it is large, but not bilobed; in others, again, it is bilobed. I have never found individual variations in respect of this matter except in the ophidioid group of species, where I think hybrids occur; this matter is dealt with elsewhere in this paper. It is not easy always to see, but I believe that the

spermathecal duct sometimes does and sometimes does not become embedded in Septum VII-VIII before penetrating the body-wall.

Genus Moniligaster, Perrier, 1872.

Prostomium never dovetailed into peristomium.

Setæ in four couples.

Clitellum develops on Segments X, XI, XII, and XIII; it is a transient structure, and does not extend over the intersegmental grooves.

Dorsal pores absent (? M. barwelli, M. beddardi).

Nephridiopores usually in the direction of the outer seta couple, but in some cases more dorsally placed in certain of the anterior segments.

Genital apertures, three pairs, all strictly intersegmental.

Male pores between Segments X and XI.

Oviducal pores between Segments XI and XII.

Spermathecopores between Segments VII and VIII.

Testes, one pair, each enclosed in a sperm-sac; they belong to Segment IX.

Sperm-sacs, one pair, provided with vascular trabeculæ; held equatorially by Septum IX-X.

Ciliated rosettes are specialised portions of the walls of the sperm-sacs.

Sperm-ducts very long and convoluted; ciliated along their whole length.

Atria, large muscular sacs.

Prostates developed as glandular walls of the atria.

Ovaries, one pair of frill-like bands in Segment XI, producing enormous numbers of eggs, which, after further growth in the ovisacs, are placed in enormous numbers in the egg-capsule, and take the place of albumen in nourishing the one or two which develop.[1]

[1] I have added this very interesting fact here because it is, in my experience, very characteristic of the genus; and I have examined the egg-capsules of three species of Moniligaster. I hope to give a fuller account of the phenomenon in a subsequent paper.

Ovisacs, one pair, developed as diverticula of Segment XI; provided with vascular walls and trabeculæ, capable of great extension.

Spermathecæ, one pair, with muscular ducts, the terminal portions of which form copulatory pouches in Segment VIII.

Nephridia paired, provided with a muscular-walled bladder; most anterior pair in Segment III; anterior pairs not modified.

Gizzard moniliform, two- to six-lobed; each lobe confined to one segment; lies somewhere between Segments XI and XXXIII.

Typhlosole absent.

Vascular System.—No portal system, i. e. peripheral veins go direct to the dorsal vessel (or hearts), while the intestinal wall is supplied by ventro-intestinal vessels; subneural present; supra-intestinal vessel may be present or absent; four pairs of hearts in Segments VI—IX.[1]

M. grandis, A. G. B., 1886.

Prostomium broad.

Size, 590 mm. long; 36·5 mm. in circumference.

Segments, 480, annulated.

Pigment, very little present.

Setæ 0·5 mm. long, dorsal gap 18 mm., lateral gaps 6·5 mm., ventral gap 5·5 mm.

Nephridiopores in Segments III to IX dorsal of the outer seta rows; elsewhere in the direction of the outer seta rows.

Male pores nearer the inner seta rows than the outer.

Oviducal pores in the direction of the inner seta rows.

Spermathecopores nearer the outer seta rows than the inner.

Septa V-VI to VIII-IX very thick.

Gizzard in five lobes, occupying Segments XVIII—XXII.

Sperm-sacs oval.

[1] I have included in this diagnosis of the genus many characters which, no doubt, properly belong to the family. The family contains at present one other genus only, viz. Desmogaster, Rosa, 1890.

Prostates hemispherical, not glandular in appearance (see p. 358).

Ovaries enclosed (see p. 357).

Spermathecæ pyriform to globular.

Copulatory pouches small, simple, embedded in the body-wall.

Vascular System.—Latero-longitudinal vessels connected with the hearts of Segment IX. No supra-intestinal vessel.

Habitat.—Nilgiris, S. India. Widely spread at elevations from 5000—8000 feet, in dry grass land; burrows to 9—10 feet, and remains coiled up at the bottom of the burrow during the dry season.

M. naduvatamensis, sp. n.

Prostomium small and pointed.

Size, 500 mm. long, 16 mm. in circumference.

Segments, 400.

Pigment absent.

Setæ 0·3 mm. long, dorsal gap 9 mm., lateral gaps 2·5 mm., ventral gap 2 mm.

Nephridiopores all almost exactly in the direction of the outer seta rows.

Male pores rather nearer the outer seta rows than the inner.

Oviducal pores in the direction of the inner seta rows.

Spermathecopores midway between the outer and inner seta rows.

Septa V-VI to VIII-IX thickened, but not so much so as in M. grandis.

Gizzard in three lobes, occupying Segments XV—XVII.

Sperm-sacs slightly kidney-shaped.

Prostates glandular in appearance.

Ovaries not enclosed.

Spermathecæ pyriform to globular.

Copulatory pouches small, simple, embedded in the body-wall.

Habitat.—Naduvatam, Nilgiris, at about 6000 feet.

Remarks.—I have only had a few specimens of this worm. It is very like M. grandis, and occurs along with that species. It is easily to be distinguished from M. grandis by its small, pointed prostomium. The whole anterior end is pointed, and when killed in spirit it is flaccid, while M. grandis is for a time very rigid.

M. nilamburensis, sp. n.

Prostomium broad.

Size, 760 mm. long, 23·5 mm. in circumference.

Segments, 566, annulated.

Pigment, very little present.

Setæ 0·63 mm. long. They appear black to the naked eye. Dorsal gap 14 mm., lateral gaps 3 mm., ventral gap 3·5 mm. Each couple is separated by 0·5 mm., and are therefore more widely separated than usual.

Nephridiopores all, I think, in the direction of the outer seta rows.

Male pores nearer the inner seta rows than the outer.

Oviducal pores in the direction of the inner seta rows.

Spermathecopores in the direction of the outer seta rows.

Septa V-VI to VIII-IX very thick.

Gizzard in five (or six) lobes, occupying about Segments XXVIII—XXXIII (normal for five lobes, the sixth lobe may be in XXVII or XXXIV).

Sperm-sacs oval.

Prostates, Ovaries, Spermathecæ, Copulatory pouches } as in M. grandis.

Habitat.—I have had preserved specimens only from Nilambur, near the sea-level, which were kindly sent me by Mr. Hadfield, of the Forest Department, who informs me that the worm burrows along in the wet season just underneath the surface.

Remarks.—This is another worm like M. grandis. It is

the only species in which I have found the gizzard so far back; in Desmogaster the gizzard occupies, according to Rosa, Segments XX—XXIX.

M. pellucida, sp. n.

Size, 90 mm. long (presents great variations, many specimens as long as 190 mm., as in the specimen figured), 9·25 mm. in circumference.

Segments, 130, not annulated.

Pigment absent.

Setæ 0·24 mm. long, dorsal gap 6 mm., lateral gaps 1 mm., ventral gap 1·25 mm. Setæ absent from Segment II.

Nephridiopores in the direction of the outer seta rows.

Male pores nearer the inner seta rows than the outer.

Oviducal pores slightly dorsad of inner seta rows.

Spermathecopores slightly ventrad of outer seta rows.

Septa V-VI—VIII-IX thickened.

Gizzard in four (or five) lobes occupying Segments XV—XVIII (XVII—XXI, XVI—XX, XV—XIX, XIV—XVII, XIV—XVIII, are not uncommon variations).

Sperm-sacs lemon-shaped.

Prostates, flattened hemispheres.

Ovaries not enclosed.

Spermathecæ lemon-shaped, in one or two specimens oval.

Copulatory pouches simple, embedded in the body-wall.

Vascular System.—Supra-intestinal vessel present, connected anteriorly with the hearts of Segment IX, which are therefore not "dorsal hearts."

Habitat.—Ootacamund and Naduvatam, Nilgiris.

Remarks.—The habit of this worm of contracting its anterior end into the shape shown in fig. 3 is very characteristic; this is the shape usually found in spirit specimens. The body-wall is very transparent.

M. uniqua, A. G. B., 1886. (Syn. M. papillatus, A. G. B., 1886.)

Size, 220 mm. long, 15·6 mm. in circumference.

Segments, 316, faintly annulated.

Pigment absent.

Setæ 0·32 mm. long, dorsal gap 8 mm., lateral gaps 2·6 mm., ventral gap 2·4 mm.; present on Segment II.

Nephridiopores closer even than usual, to the intersegmental grooves, in the direction of the outer seta rows.

Male pores between outer and inner seta rows, papilla very frequently protruded (this is the character I first noted in M. papillatus, but it is by no means specific, and this does not form a distinct species).

Oviducal pores in the direction of the inner seta rows.

Spermathecopores in the direction of the outer seta rows (between setæ 1 and 2).

Septa V-VI to VIII-IX thickened.

Gizzard in four (or five) lobes occupying Segments XVII—XX (XV—XIX, XVI—XX, XVII—XXI).

Sperm-sacs somewhat lemon-shaped.

Prostates teat-shaped, projecting rather backwards.

Ovaries not enclosed.

Spermathecæ pyriform and oval or lemon-shaped.

Copulatory pouches simple.

Habitat.—Ootacamund, Coonoor.

Remarks.—This species and M. pellucida occur together and form, I believe, hybrids,—I have found so many specimens with an intermixture of characters,—but as I dwell at length below upon hybrids in the ophidioid group, it is not necessary to do so in connection with these species.

M. chlorina, sp. n.

Size, 130 mm. long, 11·5 mm. in circumference.

Segments, 135, not annulated.

Pigment, a little present, the worm becomes greenish when put in spirit.

Setæ 0·5 mm. long, dorsal gap 6 mm., lateral gaps 2 mm., ventral gap 1·5 mm. Setæ absent from Segment II.

Nephridiopores in the direction of the outer seta rows.

Male pores nearer outer seta rows than inner.

Oviducal pores in the direction of the inner seta rows.

Spermathecopores in the direction of the outer seta rows.

Septa VI-VI to VIII-IX slightly thickened.

Gizzard in four lobes, occupying Segments XIV—XVII.

Sperm-sacs oval, rather pointed at the ends.

Prostates hemispherical, appear glandular.

Ovaries not enclosed.

Spermathecæ pyriform to oval.

Copulatory pouches small and simple.

Habitat.—Ootacamund.

Remarks.—This occurs with the two preceding species, but is very easily picked out owing to its pigment.

M. ophidioïdes, sp. n.

Size, 310 mm. long, 21·5 mm. in circumference.

Segments, 200, not annulated.

Pigment present in quantity, bluish to olive green.

Setæ 0·35 mm. long, dorsal gap 12 mm., lateral gaps 3·25 mm., ventral gap 3 mm. Couples very closely paired.

Nephridiopores mostly in the direction of the outer seta rows, those of Segments VII, VIII, and XII usually, and others occasionally, 3 mm. nearer the dorsal median line; occasionally some of the pores are in the direction of the inner seta rows.

Male pores nearer the outer seta rows than the inner.

Oviducal pores in the direction of the inner seta rows.

Spermathecopores in the direction of the outer setæ.

Septa V-VI to VIII-IX thickened but only slightly so, the most anterior of the four hardly so at all.

Gizzard in three lobes occupying Segments XIV—XVI (see remarks below).

Sperm-sacs very rounded, oval.

Prostates oblately hemispherical or, including a little more than the hemisphere, glandular in appearance.

Ovaries enclosed.

Spermathecæ pyriform and globular.

Capillary pouches bilobed, a short teat-shaped lobe in front of Septum VII-VIII, and a longer one behind the septum.

Vascular System.—The latero-longitudinal vessels are

connected with the hearts of Segment IX only; no supra-intestinal vessel.

Habitat: Ootacamund and Coonoor.

M. robusta, A.G.B., 1886. (Syn. M. indicus, Benham, 1893.)

Size, 200 mm. long, 19 mm. in circumference.

Segments 160.

Pigment present in quantity, bluish to greenish brown.

Setæ 0·3 mm. long, dorsal gap 11 mm., lateral gaps 2·5 mm., ventral gap 3 mm.

Nephridiopores, perhaps normally, all in the direction of the outer seta rows (see remarks below).

Male pores nearer the outer seta rows than the inner.

Oviducal pores in the direction of the inner seta rows.

Spermathecopores in the direction of the outer seta rows.

Septa VI-VII to VIII-IX slightly thickened, V-VI not to any appreciable extent.

Gizzard in four lobes, occupying segments XII—XV.

Sperm-sacs broadly oval.

Prostates differ in shape from those of the preceding species only in the fact that they usually lap over a little towards the middle line; glandular in appearance.

Ovaries enclosed.

Spermathecæ pyriform to oval.

Copulatory pouches bilobed, the anterior lobe larger than the posterior, and its extremity usually folded over, so as to point backwards.

Vascular System.—The latero-longitudinal vessels are connected with the hearts of Segments VIII and IX. No supra-intestinal vessel.

Habitat.—Widely spread on the Nilgiris.

M. sapphirinaoïdes, A. G. B., 1886.

Size, 140 mm. long, 17 mm. in circumference.

Segments, 160.

Pigment present in quantity, bluish-red.

Setæ 0·5 mm. long, dorsal gap 10 mm., lateral gaps 2·4 mm., ventral gap 2·1 mm.

Nephridiopores in the direction of the outer seta rows.

Male pores midway between the outer and inner seta rows.

Oviducal pores in the direction of the inner seta rows.

Spermathecopores in the direction of the outer seta rows. The nephridiopores of Segment VIII are just beyond (dorsal) the spermathecopores, and, of course, being just on the segment and not on the intersegmental groove, just behind them.

Septa VI-VII to VIII-IX very slightly thickened, V-VI not to any appreciable extent.

Gizzard in four lobes, occupying Segments XVII—XX.

Sperm-sacs oval.

Prostates, flattened hemispheres, glandular in appearance.

Ovaries enclosed.

Spermathecæ pyriform to globular.

Copulatory pouches not bilobed, but large (actually larger than they are, for instance, in M. grandis).

Vascular System.—The latero-longitudinal vessels are connected with the hearts of Segments VIII and IX. No supra-intestinal vessel.

Habitat.—Widely spread on the Nilgiris.

Remarks on M. ophidioïdes, M. robusta, and M. sapphirinaoïdes.

This group of species, which I have alluded to above as the ophidioid group, is, as a group, well characterised. The body-wall is always absolutely opaque, its muscles, especially the longitudinal muscles at the sides of the body, are well developed. They are all strong active worms which, when excited, exhibit a serpentine mode of progression; it is almost impossible to keep hold of one when excited without injuring it. Owing to the arrangement of the longitudinal muscles the body when at rest is somewhat flattened, but when in active movement becomes quite cylindrical; the tail is always capable of becom-

ing very pointed and is generally pink at the tip. The worms live in swamps and wet ground, hence no doubt the feeble thickening of the anterior septa (note in fig. 5 how the strong pharyngeal region is immediately followed in M. grandis by the four thickened septa). The intersegmental grooves are always most marked at the sides of the body, from about Segment XIV onwards. The dorsal region often has a very smooth appearance; the darker colour is, in spirit specimens (as noted by Benham), very sharply confined in this part of the body to this region; papillæ never protrude from the male pores. But when we come to diagnose species the matter becomes almost hopeless, and therefore most interesting. The trouble which I have had with this group is mainly responsible for the delay in the publication of this paper. I have at last determined to defer further examination of the matter till a future occasion. I have for the present made three species, and the diagnoses given above are the outcome of the examination of an enormous number of specimens, but the chances are about equal that any particular specimen which by external appearance I should refer to one of the three species, will or will not present an intermixture of characters. The three species are rather three types around which I can group the variations.

In connection with these variations I have considered three factors,—age, habitat, and the production of hybrids. It is difficult to altogether eliminate variations due to age. The condition of the generative organs is of course the great criterion, but the transient nature of the clitellum introduces one difficulty, and I often find specimens in which some portion of the generative apparatus, particularly the ovisacs, has a very immature look while other parts are well developed.

There is an undoubted tendency among worms to vary with even a slight difference of habitat (I have such variations recorded for future publication in connection with a Perichæte), but the variations partake in this case so markedly of an intermixture of the characters of the three types that they can, I think, only be explained by the fact that hybrids are produced, and although to make it certain the matter needs further

investigation, it has been most forcibly borne in upon me from time to time that in the specimens presenting intermixed characters there was something wrong with generative apparatus, e.g. ova not found separated from the ovary and the ovisacs in a particularly shrivelled condition, while in more typical specimens at the same time of year the ovisacs are full of ripening ova.

I have given what I consider to be the typical distinctive characters of the three species in the above diagnoses, and I now give, in the annexed table, a few particulars of some specimens of what I should call variations of M. sapphirinaoïdes among worms taken at random from one and the same locality. To carry the subject further it would be necessary to do this for each species in groups from various localities, but this would prolong this paper beyond reasonable limits, and I should like to do this at some future time on a really large scale.

Specimens 8 and 9 at any rate are immature, and they may pass as young M. sapphirinaoïdes; the setæ are rather small, but the setæ, like the exoskeleton of an arthropod, are shed at intervals and replaced by larger ones; the seta has not a permanent growth, and the full-grown embryonic seta of one of these species is 0·1 mm. long. The gizzard is far forward in them and, indeed, in all these specimens, but the normal position for M. sapphirinaoïdes has been determined by the examination of a much greater number. The condition of the ovaries and the spermathecæ in 4, 8, and 9 is due, I think, to immaturity.

Specimen 2 is what I should call a hybrid between M. sapphirinaoïdes and M. robusta,—the setæ, gizzard, and copulatory pouches resemble the latter species; the size, colouring (as in all the specimens), relative distance between the seta rows are as in the former.

Specimen 1 also resembles a M. sapphirinaoïdes, but its seta gaps have the peculiar arrangement characteristic of M. robusta.

The nephridiopores are not mentioned above; by the time I could have made certain of the position of all of them the worm

Specimen.	Length.	Length of Setæ.	Lateral Gap.	Ventral Gap.	Segments containing Gizzard.	Ovaries.	Copulatory Pouches.	Spermathecæ.
1	145 mm.	0·425 mm.	2·5 mm.	2·75 mm.	XV—XIX	Enclosed	Not bilobed	Globular and yellow.
2	130 ,,	0·225 ,,	2·75 ,,	2 ,,	XII—XVI XII small, XVI very small	Enclosed	Bilobed, anterior lobe large and folded over	Pyriform and white.
3	125 ,,	0·5 ,,	2 ,,	1·75 ,,	XVI—XX XX very small	Enclosed	Not bilobed	Globular and yellow.
4	115 ,,	0·45 ,,	1·75 ,,	1·75 ,,	XIV—XVIII	Not enclosed	Not bilobed	Pyriform and white.
5	175 ,,	0·525 ,,	2 ,,	2 ,,	XV—XX	Enclosed	Not bilobed	Globular and yellow.
6	158 ,,	0·625 ,,	2 ,,	1·9 ,,	XV—XIX	Enclosed	Not bilobed	Globular and yellow.
7	148 ,,	0·55 ,,	2 ,,	1·75 ,,	XV—XIX	Enclosed	Not bilobed	Globular and yellow.
8	97 ,,	0·4 ,,	1·75 ,,	1·5 ,,	XIV—XVIII	Not enclosed	Not bilobed, very small	Pyriform, white, and very small.
9	100 ,,	0·375 ,,	1·75 ,,	1·5 ,,	XIV—XVIII	Not enclosed	Not bilobed, very small	Pyriform, white, and very small.

would have been ruined for dissection. I quote one or two instances in which M. robusta approaches M. ophidioïdes.

M. robusta specimen—

Nephridiopores in Segments	III, IV, V, and VI . .	Outer seta rows.
,, ,,	VII and VIII	More dorsal.
,, ,,	IX, X, XI	Outer seta rows.
,, ,,	XII	More dorsal.
,, ,,	XIII	Outer seta rows.
,, ,,	XIV, XV	More dorsal.
,, ,,	XVI, XVII	Outer seta rows.
,, ,,	XVIII	More dorsal.
,, ,,	XIX onwards	Outer seta rows.

M. robusta specimen—

Nephridiopores in Segments	III—VIII	Dorsad of outer seta rows.
,, ,,	IX onwards	Outer seta rows.

My original specimens of M. sapphirinaoïdes were very iridescent, this extreme iridescence is a local variation. The clitellum in all these ophidioid species becomes pinkish in spirit.

Benham's M. indicus is probably M. robusta, or perhaps a hybrid between that and M. sapphirinaoïdes, having most of the characters of the former, and a few (including size) of the latter species. Benham says the setæ are 2 mm. long; this is surely a misprint, if not it must be a different species, or possibly a very strongly marked local variety. The specimen came, I think, from a part of the Nilgiris which I have not visited.

M. parva, sp. n.

Size, 75 mm. long, 4·25 mm. in circumference.

Segments, 115.

Pigment present in small quantity.

Setæ 0·4 mm. long, dorsal gap 2·75 mm., lateral gaps 0·75 mm., ventral gap 0·75 mm.; absent from Segment II.

Nephridiopores in the direction of seta 4, in Segment VIII just dorsal of (and behind, of course) the spermathecopore.

Male pores between the outer and inner seta rows; papillæ often protrude.

Oviducal pores in the direction of the inner seta rows.

Spermathecopores in the direction of the outer seta row.

Septa v-vi—viii-ix thickened.

Gizzard in three (four) lobes, occupying Segments xiv—xvi (xiv—xvii).

Sperm-sacs slightly kidney-shaped.

Prostates hemispherical, glandular in appearance.

Ovaries not enclosed.

Spermathecæ oval.

Copulatory pouches simple, rounded.

Vascular System.—A supra-intestinal vessel present, the hearts of Segment ix are connected with it.

Habitat.—Ootacamund.

M. minuta, A. G. B., 1886.

Size, 47 mm. long, 5·7 mm. in circumference.

Segments, 150.

Pigment, a considerable amount present.

Setæ 0·25 (to 0·15) mm. long, dorsal gap 3·6 mm., lateral gaps 1·1 mm., ventral gap 1 mm.; present in Segment ii.

Nephridiopores in the direction of the outer seta row.

Male pores in the direction of the inner seta rows (a very unusual position).

Oviducal pores in the direction of the inner seta rows.

Spermathecopores in the direction of the inner seta rows (a very unusual position).

Septa v-vi to viii-ix very slightly thickened.

Gizzard in two (three) lobes, occupying Segments xiii and xiv (xii—xiv).

Sperm-sacs oval.

Prostates hemispherical.

Ovaries not enclosed.

Spermathecæ oval.

Copulatory pouches bilobed, lobes about equal size.

Habitat.—Widely spread in the Madras Presidency at sea level and up to about 6000 feet.

M. rubra, A. G. B., 1886.

I can, unfortunately, give no further details here with regard to this species. For the present I merely place a figure of it on record.

I now give, as far as information is available, diagnoses in the form I have adopted above of the species which have been previously described by others.

M. deshayesi, Perrier (1), 1872.

Size, 150 mm. long (Perrier), "largeur 6 mm."

Nephridiopores in the direction of the outer seta row.

Male pores between the outer and inner seta rows.

Spermathecopores in the direction of the inner seta rows.

Gizzard in three or four lobes, apparently occupying about Segments XIV—XVI. Perrier describes also an anterior gizzard.

Habitat.—Ceylon.

M. barwelli, Beddard (2), 1886.

Size, about 40—50 mm. long.

Pigment, very little present in the body-wall.

Spermathecopores in the direction of the outer seta row.

Prostates oval.

Gizzard in four lobes.

Habitat.—Manila.

M. houteni, Horst (4), 1887.

Size[1] probably about 820 mm. long, about 55 mm. in circumference.

Segments, 443.

Setæ 1 mm. long; ventral gap twice the length of a lateral gap.

[1] Horst gives the length as 1500 mm., and the greatest circumference as about 55 mm. From experiments with poorly-preserved M. grandis I calculate that the natural length of M. houteni, when living and at rest, would not be less than 820 mm., a greater length than M. grandis ever attains. The circumference, where it is greatest, viz. in the anterior region, does not vary to any appreciable extent with the state of preservation and extension, as it depends upon the size of the sperm-sacs, &c.

Pigment: There is probably little pigment in the body-wall, or Horst would have mentioned the colour.

Prostates long and tubular.

Habitat.—Sumatra (Tapanoeli).

M. beddardi, Rosa (12), 1890.

Size, probably about 40 mm. long (Rosa says 30 mm., "es. piuttosto contratto").

Segments, about 115.

Setæ: Ventral gap equal in length to a lateral gap.

Pigment present.

Nephridiopores in the direction of the outer seta rows.

Male pores between the outer and inner seta rows.

Oviducal pores in the direction of Seta 2.

Spermathecopores in the direction of Seta 3.

Dorsal pores said to be present.

Septa V-VI—VIII-IX much thickened.

Gizzard in three lobes, occupying Segments XIII—XV.

Prostates pyriform.

Ovaries probably not enclosed.

Habitat.—Burmah (Chialà), at an elevation of about 4500—5500 feet.

M. japonicus, Michaelsen, 1892.

I have not seen the account of this worm.

M. bahamensis, Beddard (13), 1892.

Size, 25 mm. long.

Setæ: Judging from the figure, the lateral gaps are larger than the ventral gap; the setæ are absent from Segment II.

Male pores between the outer and inner seta rows.

Spermathecopores between the outer and inner seta rows.

Septa V-VI—VIII-IX thick.

Gizzard in three lobes, occupying Segments XIII—XV.

Prostates glandular in appearance.

Spermathecæ pyriform.

Copulatory pouches simple.

Habitat.—Bahamas.

Remarks upon previously described Species.

M. houteni differs from all my species in the long tubular prostate, about which there can be no mistake ; it is evidently more like one of the prostates of Desmogaster. With regard to the numbering of the segments I say nothing.

M. barwelli has been described piecemeal, and even now I am unable to be quite sure whether it is the same as M. minuta. I presume not, as the spermathecopores are in a different position.

M. beddardi is obviously not M. parva, and it could be no other known species.

M. deshayesi is lost in obscurity, and unless by means of the type specimen there will be little chance of identifying it. I have found one species of Moniligaster in Ceylon among some thirty species of other genera, so that Moniligaster is not the dominant genus in Ceylon, even in the hills, that it is in S. India (at any rate on the Nilgiris). My notes of this Ceylon specimen are insufficient. I refrain, therefore, from naming it at present, and give an external figure only, for future reference. Its colouring distinguishes it from all my other species. The gizzard occupies Segments xv—xviii. I obtained one specimen only at Kandy.

M. bahamensis is at present very insufficiently characterised. I have gathered most of the characters mentioned above from the figures.

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EXPLANATION OF PLATES 22—28,

Illustrating Professor A. G. Bourne's memoir "On Moniligaster grandis, A. G. B., from the Nilgiris, S. India; together with descriptions of other species of the genus Moniligaster."

PLATE 22.

FIG. 1.—Moniligaster grandis. The entire worm drawn from life, natural size. This was the largest specimen I ever found. The clitellum extending over Segments X, XI, XII, and XIII is much better marked than in the majority of individuals during life. The tail had been regenerated.

FIG. 2.—Moniligaster grandis. Ventral view of the thirty-six most anterior segments drawn from life from a smaller specimen. *sp.* Position of the spermathecopores. ♂, ♀. Position of the male and oviducal pores. *i. s.* Letters with reference lines, inserted to show that the structures so marked represent inner seta couples.

PLATE 23.

Entire worms drawn from life, natural size. *cl.* Clitellum.

FIG. 3.—Moniligaster pellucida. The anterior end is shown in the characteristic form it assumes when contracted.

FIG. 4.—Moniligaster uniqua.

FIG. 5.—Moniligaster chlorina.

FIG. 6.—Moniligaster ophidioïdes.

FIG. 7.—Moniligaster robusta. From *r.* onwards the tail had been regenerated.

FIG. 8.—Moniligaster sapphirinaoïdes.—A typical specimen from very wet ground at Naduvatam showing the iridescence.

FIG. 9.—Moniligaster sapphirinaoïdes-robusta. An example of a worm with external and internal characters intermediate between those of the two species, probably a hybrid.

FIG. 10.—Moniligaster sapphirinaoïdes-ophidioïdes.—An example of a worm with external and internal characters intermediate between those of the two species, probably a hybrid.

FIG. 11.—Moniligaster parva.

FIG. 12.—Moniligaster minuta.

FIG. 13.—Moniligaster rubra.

FIG. 14.—Moniligaster *sp.* From Ceylon.

PLATE 24.

Moniligaster grandis.

Fig. 15.—Ventral view of the head end. Segments numbered I—XV. *i. s.* Inner seta couples. *cl.* Clitellum. *Sp. apt.* Spermathecopore. ♂. Male pore. ♀. Oviducal pore. The prostomium entirely withdrawn.

Fig. 16.—Lateral view of the head end. Segments numbered I—XI. *n.* 3 to *n.* 11. Nephridiopores. *o. s.* Outer seta couples. *pr.* Prostomium fully extended along with the buccal membrane. *Sp. apt.* and ♂ as before.

Fig. 17.—Diagrammatic vertical longitudinal section of the anterior Segments I—XIV. The italic roman numerals *III—XII* are placed in the cavities of the several segments. 7/8—12/13. Septa bounding various segments. *pr.* Prostomium. *m.* Muscular pad in the dorsal wall of the pharynx. *Sal. gl.* Salivary glands. *Sp.* Spermatheca. *Cop.* Copulatory pouch. *Sp. apt.* Spermathecopore. *Sp. sac.* Sperm-sac. *T.* Testis. *f.* "Ciliated rosette." *V. d.* Seminal duct. ♂. Male pore with the prostate and atrium. *Ov.* Ovary. ♀. Oviducal pore with the oviduct. *Ovs.* Ovisac.

Fig. 18.—Ordinary epidermis. *Cu.* Cuticle. *Ep.* Unmodified epidermis cells. *gob.* Gland-cells.

Fig. 19.—Clitellar epidermis. *S. cl.* Short club-shaped cells. *l. cl.* Long club-shaped cells.

Fig. 20.—Epidermis cells from the neighbourhood of the genital apertures.

Fig. 21.—Epidermis cells from an intersegmental groove.

Fig. 22.—The gizzard in longitudinal section. The septa bounding Segments XVIII—XXII are indicated. *giz.* The annular muscular bands. *musc.* The outstanding muscle fibres. *Oe.* The soft-walled portions between the annular muscular bands.

Fig. 23.—Surface view of a portion of the gizzard to show the outstanding muscle fibres. Letters as before.

Fig. 24.—From a longitudinal section of the intestinal wall in the region of the tubular glands. *gl.* The glands; the section passes through the aperture of one into the intestine. *Cœl. ep.* Cœlomic epithelium. *Al. ep.* Intestinal epithelium. *V.* Blood-vessels. (Leitz, ocular 3, obj. 3, cam. luc.)

Fig. 25.—Longitudinal section at the anal extremity to show the thickened septa. *Ep.* Epidermis. *Al. ep.* Rectal epithelium. *Sept.* Septum. At *an.* is the anus.

Fig. 26.—A seta couple. One being a little more bent over than the other, appears a little shorter.

PLATE 25.

Fig. 27.—M. grandis. A dissection of the anterior region. The segments as defined by the intersegmental grooves are marked VI to XIV. Certain of the segments as defined by the septa are marked *IX*, *X*, *XI*, *XII*. The cut edges of certain septa are marked 9/10, 10/11, 11/12. *o. s.*, *i. s.* Outer and inner seta lines.

Nervous System.—The cerebral ganglion, œsophageal commissures, the ventral nerve-cord, and some of the nerves are shown. In the cerebral ganglion the bilobed ganglionic mass is shown surrounded by the sheath. *N. Pro.* Prostomial nerves. N. I, N. II, &c. Nerves belonging to the Segments I, II, &c. The five pairs of nerves to the œsophageal wall are shown. A small portion of the thick septum 7/8 is left undissected away to show the anterior nerve of Segment VIII passing into its substance. The nerves in most segments are shown only up to the inner seta line where they pass into the muscular layers, but in Segment IX and a portion of Segment X these are dissected away to show the distribution of the nerves. *n.* 1, *n.* 2, *n.* 3. The three nerves of the segment. *n. sept.* Branches supplying the septum. *n. v.* Nerve to the viscera of the segment. *n. x.* Nerve joining *n.* 3 with the septal nerve of the next following segment. Some portion of the septa 9/10, 10/11, 11/12 having been left, the nerve-cord disappears for a time in Segment X to reappear in Segment XII (as defined by the septa, the great development of the lumen of Segment XI throws this region back to Segment XIV, as defined by the intersegmental groove). The curved arrow shows where the nerve-cord passes into Segment XII, and then under Segment XI. As a matter of fact, if Segment XI was filled with ova, &c., not only the nerve-cord but the ventral vessel and the œsophagus would not be seen in this region.

Nephridia.—The position of the external apertures of the nephridia of Segments III to XII are shown on the right-hand side; of Segments IX to XIII on the left-hand side, and marked by a small circle with the numbers 3, 4, 5, &c., by the side. In the case of the nephridia of Segments X—XIII a small portion of the excretory duct is drawn to show how the ducts of the nephridia of Segments X and XI carry the septum forward to its true position. On the left-hand side the marks *n.* 3, *n.* 4, *n.* 5, &c., enclosed by a line, indicate the nephridia supplied by the blood-vessels which touch the line in question.

Vascular System.—The exact arrangement of the vessels must be followed from the text. Note:—The ventral vessel, V. V.; the branches, Br. V. T., of the ventro-tegumentary vessels of Segments I and II; the ventro-tegumentary vessels, V. T., of Segments III, IV, and V, the latter supplying, besides the body-wall, &c., the salivary glands (vessels marked *Sal.*) and the nephridia of those segments; the ventro-intestinal vessels V. I., the most anterior one in Segment VI; the "ventro"-tegumentary

vessels, V. T.′, of Segments VI, VII, and VIII, which arise not from the ventral vessel, but from the hearts of those segments; the ventro-tegumentary vessel, V. T.″, which arises from the heart of Segment VIII and supplies Segments, IX, X, part of XI, the nephridia of those segments, the sperm-sacs (*Sem.*), the prostate (*pr.*), and the ovaries (*ov.*); the ventro-tegumentary vessel of Segment X (V. T.‴) supplying only the ovary, which thus receives a double supply; the ventro-tegumentary of Segment XII, the arrangement of which may serve as a type for those vessels in the rest of the body. Note also the hearts (H. VI.—H. IX.), shown cut short with some of the vasa-vasorum upon their walls. Note also the latero-longitudinal and subneural system, coloured blue. The three big trunks are seen to join together just behind septum 9/10 where the main trunk (shown cut short) passes upwards to open into the hearts of Segment IX (cp. fig. 33). The anterior and outer posterior trunks are seen to collect blood carried outwards by all the branches of the ventral vessel and hearts (except the hearts themselves) of Segments I to IX; the inner posterior trunk is connected with the subneural vessel (not shown) by vessels marked *a* and *b*; with it is also connected the "veins" of Segments XI and XII. Except for the connection just mentioned, the "vein" of Segment XII, really a branch of the subneural, serves as a type of the arrangement of these vessels in the rest of the body; it is joined at *z* by the dorso-tegumentary vessel of the segment (D. T.), and passes on from *c* to the subneural.

All the vessels are drawn in as accurately as possible as far as they go. I have been unable to make quite sure about the ventro-intestinal of Segments X, XI, and XII. I think there are no such vessels in Segments X and XI and a pair as usual in Segment XII, but these are not drawn. The nephridiopores of Segments IX—XIII are specially inserted on the left-hand side to show the relation of the blood-vessels to them.

Generative Organs.—These are only indicated to show their relation to the various segments and septa. ♂ and ♀. Male and female pores. *Sp. sac.* Sperm-sac. *pr.* Prostate. *Ov.* Ovary. *ovd.* Oviduct. *ovs.* Ovisac. *Sp.* Spermatheca. *cop.* Copulatory pouch dissected out.

Fig. 28.—M. ophidioïdes. Plan of the blood-vessels in a segment in the region of the gizzard, *giz.* D. v. Dorsal vessel. *D. Teg.* Dorso-tegumentary vessel; this joins the branch of the subneural at *z*. *D. Int.* Dorso-intestinal vessel; its branches are seen to emerge from the gizzard wall and then join together. *V. Teg.* Ventro-tegumentary vessel; this passes round towards the dorsal region, giving off branches to the nephridium, *Neph.*, and body-wall; all the blood distributed by it is carried back to the subneural by a branch of that vessel, *Br. S. N.*

Fig. 29.—M. ophidioïdes. View of a portion of the latero-longitudinal and subneural system. *S. N.* Subneural vessel; the most anterior branches of this to receive dorso-tegumentary vessels are those of Segment XV; the

dorso-tegumentary vessel joins the subneural branch at *z*. The latero-longitudinals *a. b.*, *a. b.* have come down at *a. a.* from the head region; all the blood brought forward by the subneural passes into them; more blood always passes on the right side than on the left; all this blood is carried by *c.*, *c.*, *c.*, *c.* into the hearts of Segments VIII and IX. The subneural itself is seen to come to an end shortly after giving branches to the latero-longitudinal vessels. What little blood gets into this anterior prolongation must be carried backwards to pass into the latero-longitudinal.

FIG. 30.—M. pellucida. View of the supra-intestinal vessel, S. I., and its branches. The dorsal vessel is not drawn; it has no connection in this species with the hearts of Segment IX (H. IX). The supra-intestinal arises on the gizzard at *f.*, and receives vessels from the walls of that organ and from those of the œsophagus in front, *d.*, *d.* It also receives all the blood from the latero-longitudinal and subneural vessels by *e.*, *e.* It then bifurcates and empties its blood into the hearts of Segment IX. *a.* Latero-longitudinal vessel from the head region. *b.* Portion of the latero-longitudinal which is connected with the subneural. *c.* Vessels from the sperm-sacs. *sp.* Prostates, &c.

PLATE 26.

FIG. 31.—M. grandis. Diagram of the vessels in any Segment from XII onwards. B. w. Body-wall. INT. Intestine. On the right hand is shown the nephridium. *n.* The nephridiopore. The setæ are shown in their right position with regard to the gaps. The dorsal blood-vessel, D. V., is shown with its dorso-tegumentary branch D. T., and its dorso-intestinal branch, D. I. The former joins the branch of S. N., the subneural, at z. The ventral vessel, V. V., is shown with its ventro-tegumentary branch, V. T., and its ventro-intestinal branch, V. I. n., n., n. Nephridial arteries and veins.

FIG. 32.—M. grandis. Diagram of the vessels in Segment VII. The heart is shown on the left side with the muscular bulb interposed between it and the ventral vessel, V. V. The ventro-intestinal branch is shown going to the œsophageal wall. The ventro-tegumentary vessel is shown arising from the heart just beyond the muscular bulb, giving off a branch to the heart-wall (this passes on to the wall of the dorsal vessel also) and branches to the body-wall. The main trunk of the latero-longitudinal and subneural system, viz. the anterior latero-longitudinal vessel, L. L., is shown in its proper position, and is seen to receive veins from the œsophageal wall and the wall of the heart and the body-wall.

FIG. 33.—M. grandis. Diagram of some of the vessels of Segment IX to show the latero-longitudinal vessels (each now composed of its three branches, anterior and two posterior, *cp.* fig. 27) passing downwards and

opening into the hearts of this segment. Their connection, and that of the hearts, with the dorsal vessel is also shown.

Fig. 34.—M. grandis. Diagram of the arrangement of the blood-vessels on one side of a segment. The ventro-tegumentary vessel and the branch of the subneural are seen playing opposite rôles. The dorso-tegumentary is seen to join the branch of the subneural at *z*. The meaning of the various arrows is explained in the text, p. 335.

Fig. 35.—M. sapphirinaoïdes. Small arteries and veins in the body-wall seen in a longitudinal section. *Sept.* Septa. *Ep.* Epidermis. *Cm.* Circular muscular layer. *l. m.* and *l.* m^2. Inner and outer longitudinal muscular layers.

Fig. 36.—M. sapphirinaoïdes. Portion of the epidermis from the same section as in the preceding figure. The actual "capillaries" are seen.

Fig. 37.—M. grandis. Blood-vessels on a portion of the nephridium.

Fig. 38.—M. grandis. Diagram of the arrangement of the blood-vessels in the intestinal wall. Letters as before. The arrows show the direction of the blood-flow.

Fig. 39.—M. grandis. Portion of the dorsal vessel cut open in the dorsal median line to show the apertures of the dorso-tegumentary and dorso-intestinal vessels. *x.* Valve preventing backward flow in the dorsal vessel. *y.* Valve at the mouth of the dorso-intestinal vessel preventing outward flow.

Fig. 40.—M. grandis. View of the hinder surface of septum 7/8. The relative positions at which the œsophagus, *Oe.*, the dorsal vessel, D. V. the ventral vessel, V. V., the latero-longitudinal vessels, *L. L.*, and the nerve cord, *n.*, pass through the septum are shown. The spermatheca, *Sp.*, and its duct are shown. The spermathecal duct penetrates the septum at *x.* and runs in the thickness of the septum, as shown by the dotted lines, to the copulatory pouch, which is embedded in the thickness of the body-wall. The setæ are inserted, although, of course, they really lie further forward.

Fig. 41.—M. grandis.—Diagram of a section across the body in Segment VII to show the "mesenteries" marked by thick black lines (each really double) which join the longitudinally running vessels to the intestinal and body-walls. Letters as before.

PLATE 27.

Moniligaster grandis.

Fig. 42.—Plan of an entire nephridium of the left-hand series, drawn as though the worm were opened along the dorsal median line and flattened out. *V. V.* Position of the ventral median line. *i. s.*, *i. s.*; *o. s.*, *o. s* Inner

and outer seta lines. The position of the septum bounding anteriorly the segment which contains this nephridium, at the place where the nephrostomial duct perforates it, is shown at *sept.*, so that the vesicle and adjoining portions of the nephridium are supposed to have been turned forwards. The greater part of the gland is shown in optical section; but at certain places, left unshaded, a view nearer the surface is taken. This will be intelligible on a comparison with the text. *st.* Nephrostome. *st. a.* Nephrostomial duct. This duct joins the rest of the gland at *a*. The duct which passes from *a* to *b* is shown in three places in the surface views, and marked "*ab*." The duct which passes from *b* to *c* is shown in three places, and marked "*bc*." The duct passing from *c* to *d* is marked "*cd*." The duct passing from *d* to *e* is marked "*de*." The duct passing from *e* to *f* is marked "*ef*." The duct passing from *f* to *g* is marked "*fg*." The vesicle duct passing from *g* to *h*, the point where it opens into the vesicle is marked "*gh*." *ves.* Vesicle; the muscles shown in a portion of its walls only. *j.* Sphincter muscle. *ex. apt.* Place where the excretory duct penetrates to the body-wall to pass to the nephridiopore.

Fig. 43.—A nephrostome, fixed and stained, showing forty-five marginal cells, two nuclei of central cells, and at the margin the flattened nuclei of cœlomic epithelium cells.

Fig. 44.—Section through a nephrostome, with a portion of the duct, showing a nucleus, *c*, of a central cell and a nucleus, *m*, of a marginal cell.

Fig. 45.—Portion of a nephridial ductule with undulating bundles.

Fig. 46.—Surface view of a portion of the nephridium in the region "*ab*," drawn from a freshly mounted preparation.

Figs. 47 and 48.—Transverse sections of the ventral nerve-cord. Fig. 47, from an interganglionic region; Fig. 48, passing through a ganglion and through the origin of one of the nerve branches on one side. The two figures drawn with the camera lucida to the same scale. *ep.* Cœlomic epithelium. *c. t.* Connective-tissue sheath. *s.* Space left owing to the contraction of *h.*, the hyaline sheath, in which are embedded the muscles, *musc.* *g. f.* Giant fibre. *n. f.* Nerve fibres. *ngl.* Neuroglia. *gang.* Ganglion cell. *v.* Blood capillaries.

PLATE 28.

Moniligaster grandis.

Fig. 49.—View of a dissection to show the bands of muscle, *m.*, which are connected with the body-wall in the neighbourhood of the male pore (? copulatory muscles). *N. c.* Nerve-cord, with the three nerves, 1, 2, 3, of Segment X and the first nerve of Segment XI. Septum 9/10 is turned forward, and Septum 10/11, to which is also attached Septum 11/12 (not shown) is turned

backward. The excretory ducts of the nephridia of Segments X and XI, *neph.* 10, *neph.* 11, are shown. *pr.* Prostate. *v. d.* Sperm duct. *o. s.*, *i. s.* Outer and inner seta lines.

FIG. 50. Diagrammatic drawing from a thick longitudinal section to show the relations of the oviducal wall, *ovd.* Other letters as before.

FIG. 51.—The ovisacs, *ovs.*, and the portion of Segment XI which contains the ovaries filled with ova, drawn the natural size.

FIG. 52.—"Ciliated rosette," as seen on opening the sperm-sac. The portion of the sperm-duct drawn is seen through the wall of the sac.

FIG. 53.—Sperm-duct in transverse section. A loop bound together by the connective tissue of the "mesentery," the duct cut across twice.

FIG. 54.—Portion of the sperm-duct in longitudinal optical section. *c. t.* Connective tissue. *ep.* Epithelium.

FIG. 55.—Longitudinal section passing through the papilla protruded at the male pore. *at.* Atrium. *pr.* Prostate. *musc.* Muscle covering the prostate. *v. d.* Sperm-duct about to open into the atrium.

FIG. 56.—Small portion of the same section more highly magnified, showing the gland cells of the prostate and their ducts.

FIG. 57.—From a section across the ovary, *ov.*, including a portion of the oviducal wall. This shows the epithelium of the oviduct becoming continuous at *a.* with the cœlomic epithelium.

FIGS. 58 and 59.—Longitudinal sections from a young individual 140 mm. long. *T.* Testis. *f.* Ciliated rosette. Other letters as before. The copulatory pouch is not yet developed.

A Review of Professor Spengel's Monograph on Balanoglossus.[1]

By

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With Plates 29 and 30.

The eighteenth monograph of the Naples series lies at length before us. As a monument of patient industry and a mine of anatomical facts it stands in the foremost rank of zoological treatises. It contains minute descriptions of all the known species of Balanoglossus, as well as complete discussions, not only as to the relationship of this interesting form to various phyla of the animal kingdom, but also as to the special morphology of every organ in the body of Balanoglossus.

As the conclusions at which Professor Spengel has arrived are at variance with the views as to the relationship of the Enteropneusta which have been widely held in England for the last ten years, it seemed to me that a short account of the principal additions to our knowledge contained in the monograph might be useful to zoological students who lack the time necessary to peruse so huge a tome as the one before us.

I shall append to the account of the new facts brought to light a short discussion on Professor Spengel's views as to the phylogenetic position of the Enteropneusta, as it seems to me that he has adduced nothing which militates in the slightest

[1] "Die Enteropneusten des Golfes von Neapel und der angrenzenden Meeresabschnitte," J. W. Spengel, 'Series of Naples Monographs,' No. 18.

against the view now so widely accepted as to the Vertebrate affinities of the group.

Before entering on the new points contained in the monograph it will be necessary to give a rapid sketch of the history and the extent of our present knowledge of the anatomy and development of Balanoglossus. Kowalevsky[1] was the first who gave a tolerably correct account of the anatomy. Our knowledge on this point was almost completed by Professor Spengel's[2] preliminary account in 1884. Between the years 1884 and 1886 Bateson[3] contributed a series of papers on the development and morphology of Balanoglossus, which laid a solid foundation for the interpretation of the anatomical facts as indicative of Vertebrate affinities. Quite recently Morgan[4] has published a paper on the growth and development of Tornaria, which entirely confirms Bateson's account, making allowance for the difference between direct and free larval development; and Marion,[5] Schimkewitsch,[6] and Köhler[7] have given during the last few years descriptions of different species.

Fig. 1, Pl. 29, is a diagram representing a horizontal section through an adult. We notice that there are three regions to be distinguished in the body, viz. the præoral lobe or proboscis, the thick "collar" region, and the trunk. The proboscis region is largely filled with muscle, but it also contains a small cœlomic space opening on the left by a ciliated pore. The collar and trunk both contain a pair of such spaces, and the

[1] "Anatomie des Balanoglossus delle Chiaje," par A. Kowalevsky, in 'Mém. Acad. Imp. Sc. St. Pétersbourg,' 1866.

[2] J. W. Spengel, "Zur Anatomie des Balanoglossus," 'Mitt d. Zool. Station z. Neapel,' Bd. v, 1884.

[3] Bateson, "Development of Balanoglossus," various papers, 'Quart. Journ. Micr. Sci.,' 1884—1886.

[4] T. H. Morgan, "Growth and Development of Tornaria," 'Journal of Morph.,' vol. v, 1891.

[5] A. F. Marion, "Sur deux espèces de Balanoglossus," 'Arch. Zool. Exp.' (2), Tome iv.

[6] Schimkewitsch, "Ueber Balanoglossus Mereschkovski," 'Zool. Anz.,' 1888.

[7] R. Köhler, "Contributions à l'Étude des Entéropneustes," 'Inter. Monatsschrift Anat. Hist.,' Bd. iii, Heft 4.

collar cœlom on each side opens by a short ciliated canal into the outer part of the first gill-slit. Projecting into the proboscis cœlom from behind we observe a spongy mass of tissue with blood-vessels, Bateson's proboscis gland, which is without doubt an excretory organ. Posterior to this again, is a vesicle (*Pc.*), the sac of the proboscis gland, immediately behind which we see the heart. This last communicates by a narrow slit with the great dorsal vessel. The alimentary canal commences just posterior to the proboscis with a ventral mouth; its first portion in the collar region constitutes a simple buccal cavity; the next part in the anterior part of the trunk bears a series of pairs of gill-sacs opening to the exterior by pores situated dorsolaterally. Immediately ventral to these openings we see the openings of the gonads, the sexual glands in both sexes being represented by a series of simple or branched sacs opening directly to the exterior.

Fig. 2 on the same plate represents a diagrammatic sagittal section of the animal. We notice that the alimentary canal in the trunk region is differentiated into two tubes—a lower one called the œsophagus (sensu stricto), and an upper one, the branchial tube, into which the gill-sacs open. We notice also that the inner openings of these are elongated vertically, and almost completely divided by a projection from their dorsal edge, the tongue-bar; the outer gill-pores (*Brex.*), on the contrary, are simple circular openings. In the collar region, dorsal to the blood-vessel, we see a longitudinal band of tissue connected before and behind with an invagination of the ectoderm. This is the central nervous system, and it is connected with the dorsal ectoderm by three cellular strands, the dorsal roots. In its interior are a series of small isolated cavities lined by columnar cells. In the front part of the collar region a dorsal diverticulum of the pharynx is seen reaching far forward into the base of the proboscis, and underlying the heart and sac of the proboscis gland. This is the notochord; it has a cuticular sheath, which is largely thickened, ventrally giving rise to a chitinous skeletal rod. A portion of this rod is secreted by the inner ends of the ectoderm cells on the base of the proboscis; be-

tween the ectodermic and notochordal portions a wedge of tissue projects—really the modified tip of the ventral pocket of the proboscis cœlom (*Pr. cœ. v.*) ; Köhler, however, mistook it for a blood-vessel, and described the skeletal rod as completely divided into two by vascular tissue. In fig. 2 the great ventral vessel is seen as well as the dorsal. Fig. 3 is a transverse section through the base of the proboscis, showing the mutual relations of heart, notochord, proboscis gland, and proboscis cœlom. Fig. 4 is a transverse section through the collar region, the main point to notice being that the dorsal vessel has on each side of it a space half filled with muscular tissue—the peri-hæmal cavity (*PH.*). This, as can be seen in Fig. 1, is a forward diverticulum of the trunk cœlom.

Fig. 5 is a transverse section through the branchial region of the trunk. The figure-of-8 form of the alimentary canal is well seen, the upper part being the branchial tube, the lower the œsophagus. Where the one passes into the other there is on each side a ridge of thickened epithelium, and in life these two ridges are closely apposed, entirely separating the two tubes. The tongue-bar is seen on each side of the branchial tube in longitudinal section, and is seen to contain a portion of the trunk cœlom. On each side of the dorsal surface is seen a slight projection—the genital wing—in the proximal part of which the gonad opens on each side. Sections of the dorsal and ventral vessels are seen, and also of the dorsal and ventral nerve-cords. The whole ectoderm is ciliated, and has a well-developed plexus of nerve-fibrils amongst the bases of its cells. The dorsal and ventral nerve-cords are mere local thickenings of this plexus: the latter is confined to the trunk region; the former, however, passes into the posterior end of the central nervous system through the posterior ectodermic pit. Just behind the collar a ring of nervous matter puts the dorsal and ventral nerve-cords in communication with each other. The nerve-plexus is well developed in the proboscis region, and is especially thick round the narrow neck by means of which the proboscis joins the collar, constituting a kind of anterior nerve-ring.

The development has been worked out by Bateson as mentioned above, the main points observed being the following:— The egg undergoes total and regular segmentation, and forms a one-layered blastophere. Regular embolic invagination follows, giving rise to a gastrula, and the blastopore is situated posteriorly and slightly dorsally. It closes in the position about where the future anus is formed. The archenteron gives rise to an anterior and to two lateral pairs of pouches, as shown in fig. 6; the former becomes proboscis cœlom, the latter the collar and trunk cœlomic cavities. The notochord arises partly as an anterior diverticulum of the gut; its posterior part, however, is constricted off as a dorsal groove of the buccal cavity. The central nervous system is separated from the ectoderm by delamination, but is added to anteriorly and posteriorly by fore and aft invaginations from the anterior and posterior surfaces of the collar. The species on which Bateson worked develops up to a comparatively advanced stage within the egg-membrane, and hence its external larval characteristics have been very much modified. The ordinary mode of development seems to be through a most interesting pelagic larva, Tornaria, the early history of which is unknown. This larva shows a very close resemblance to the Bipinnaria larva in the disposition of its cilia and in the possession of a præoral cœlomic vesicle opening by a pore on the left side, whereas in the position of a well-marked apical plate, connected by a double muscular band with the sides of the œsophagus, it recalls certain features of the trochosphere. Morgan has made the interesting observation that the central nervous system in this larva is formed by the invagination of a strip of ectoderm exactly as in Amphioxus.

The monograph of Professor Spengel commences with a detailed description of one of the Neapolitan species, which is chosen as a type. The other species are then described in the order of their affinity to this type. Next follows a chapter on the ontogeny. Then the special morphology of each organ is discussed in detail. To this succeeds a chapter on the general morphology of the animal, and finally there is a discussion of

the various theories as to the relationships of Balanoglossus which have been put forward, together with an exposition of Professor Spengel's own views on that subject.

Confining ourselves in the first instance to the purely anatomical portion of the treatise, the main interest which attaches to Professor Spengel's work is the proof he has given as to the extent to which homologous organs may vary within a small sharply circumscribed group; in other words, it is especially valuable from a systematic point of view. There are, however, several points of general interest which he has brought out which must be first dealt with. These concern the vascular, muscular, and skeletal systems.

The vascular system is, according to Professor Spengel, nothing else than a system of communicating spaces and clefts devoid of any proper wall, the remnants of the embryonic segmentation cavity. Their muscular coat, when they have one, is derived entirely from the neighbouring organs. Thus the trunk cœlom supplies longitudinal and circular muscles to the dorsal and ventral vessels. The main part of the vascular system is in the form of a very close dermal plexus, and of a similar one between the splanchnic muscles and gut epithelium. These plexuses are connected with each other through the dorsal and ventral trunks by vessels running in the dorsal and ventral mesenteries. In the trunk the ventral vessel takes up the whole extent of the mesentery, and is in open connection with the enteric plexus. The ventral vessel is joined to the dorsal just behind the collar by a specially wide ring-shaped sinus. The musculature of the heart is supplied by the ventral wall of the vesicle, which Bateson called the sac of the proboscis gland. Spengel has, however, shown that it is an entirely closed vesicle, having no connection with the proboscis gland whatever. It is the same as the so-called "heart," or pulsating vesicle of the Tornaria. Spengel calls it "Herzblase"—a term which I have ventured to translate "pericardium." The true heart[1] is a space between this vesicle and the notochord; it communicates by a

[1] Spengel calls this space the central blood-space, and refuses the term heart to it on the ground that it is a mere split, and that its muscles are derived

very narrow channel with the dorsal vessel, and by several chinks with the proboscis gland. The structure of the latter is explained in a beautifully lucid manner; it consists of nothing but the posterior epithelial wall of the proboscis cavity, which is pushed forward into the cavity by the forward growth of the notochord. It is thrown into folds, to which correspond wide blood-vessels connected with each other in a net-like manner. The epithelium covering them consists of large pale cells with often concretions of yellow granules, probably excretory in nature. Blood is apparently carried from it by two lateral vessels, which run along the notochord to the buccal cavity. Here they run first obliquely and then vertically downward, and unite underneath the gut to form the ventral plexus of the collar region, which opens behind into the ventral vessel.

The blood-supply of the gill-sacs is only part of the enteric plexus; it is specially richly developed around the inner opening of the gill-sacs, which appear to be their functionally active part. Special vessels arise from the dorsal vessel (see fig. 2) to join this network.

The blood is a coagulable fluid, and contains abundance of those wandering cells or amœbocytes which are found in all Metazoa, from the medusa to man inclusive. In Ptychodera, the most differentiated genus, they appear to have given rise to a continuous endothelium in the larger vessels, but no trace of this is seen in the more primitive species.

The skeletal system next claims our attention. There is no cuticle in the Enteropneusta; the entire surface of the skin (with the exception of discharging gland-cells) is ciliated, and the same remark applies to the gut-cells. The cells lining the U-shaped inner openings of the gill-sacs have powerful cilia. The Enteropneusta, however, unlike all Annelids and Arthropods, possess to a great extent the power of secreting cuticular or "ground" substance from the inner or basal ends of the cells composing the various epithelia. Spengel calls this substance

from the pericardium; but, as appears from his own description, similar remarks apply to the whole of the vascular system.

"Grenzmembran," implying that it is only found where two tissues meet; but it seems to me that he unnecessarily obscures its nature by this mode of expression: since he allows that it is in this "border membrane" that the blood-vessels are perforated, it follows that the excretions of two epithelia are sometimes separated by a remnant of the blastocœle. This cuticular substance is specially thickened (being deposited in the form of concentric layers) to form the skeletal rod underlying the notochord, and the skeleton supporting the U-shaped gill-slits. The latter, as being the simpler, will be explained first. Adjacent gill-sacs are apposed along their inner borders. This region is called by Spengel a gill septum. The apposed epithelia give rise to a septal bar; this shows, however, its double nature by a longitudinal furrow, and by diverging below into two. The "tongue," as we have seen, contains a portion of the cœlom, and hence it gives rise to two bars, which owe their existence mainly to the epithelium of the gill-sac, though the cœlomic mesoblast contributes also to a certain extent. Each septal bar is connected by a dorsal arch with the posterior bar of the tongue in front, and the anterior one of the tongue behind, so that the entire gill-skeleton consists of a number of three-pronged bars, as shown in Pl. 29, fig. 13*a*.

To understand the relations of the skeletal rod underlying the notochord we must glance for a moment at the structure of the notochord itself as shown in fig. 2. We can distinguish in it a neck and a head portion. The former opens into the buccal cavity behind, and has a comparatively wide lumen throughout. The latter is almost solid (Bateson stated that it was quite solid, but Spengel maintains the existence of a narrow lumen), and runs out under the heart, pushing the epithelium of the proboscis cœlom before it, thus giving rise to two ventral pockets of this cavity (*Pr. v. m.*) separated by a septum. Behind, where the head joins the neck, it gives rise to a ventral sac with a widish lumen. Now the main portion of the skeletal rod is a cuticular excretion of the cells of the ventral side of the neck and the posterior aspect of the ventral diverticulum of the head; the ectoderm of the ventral side of

the proboscis stalk, however, also gives rise to skeletal matter, which behind fuses with the notochordal excretion, but in front is separated from it by a wedge of cells, the solid tips of the ventral pockets of the proboscis cavity. This ectodermal rod is called by Spengel "the tooth of the skeleton" (Pl. 30, fig. 9 *T.*). The notochordal skeleton is thinnest in front, where it supports the ventral wall of the ventral sac of the notochord, and thickest under the neck portion. Where the neck passes into the buccal cavity the skeletal rod splits into two rods, which pass to the right and left of the buccal cavity embedded in slight lateral grooves in the wall of the same, to whose cells they owe their existence. Now Bateson maintained that the hinder part of the notochord was pinched off from the gut-wall by lateral grooves, and Spengel has been able to supply a most interesting confirmation of this idea. If we cut sections of the hinder part of the undivided skeletal rod, we find that whereas the younger layers are arranged concentrically round a single centre, the older layers form two systems of concentric curves round two separate centres to the right and left respectively of the new centre. Hence where now the skeleton is a single rod secreted by the ventral wall of the notochord, it used to be in the form of two rods lying in grooves of the lateral walls of the buccal cavity, but these grooves have coalesced and separated off the notochord. Pl. 30, figs. 8—13, show the form of the collar skeleton in several of the species.

In addition to this primary skeleton there is developed in all species, though much more in some than others, a supplemental skeleton, the chondroid tissue. It is the special merit of Marion to have first called attention to this tissue.

It consists of a structureless ground substance with numerous groups and strings of cells embedded in it, presenting in transverse section a strong resemblance to cartilage. In longitudinal section, however, it is seen that these cellular masses are outgrowths from the walls of the collar cœlom, and in some cases also from the wall of the d o r s a l pockets of the proboscis cavity (i. e. the portion of the proboscis cavity which ends in the pore and the corresponding blind portion on the right).

In nearly all cases there is a small portion of this tissue also derived from the ventral pocket; this projects, as we have seen, into the niche left between the tooth and body of the primary skeleton.

Professor Spengel gives a detailed description of the muscular system. It gives characters which are of great use from a systematic point of view; but here we need only notice a point or two of general interest. There is no dermis of connective tissue; immediately beneath the epidermis is a basal membrane of cuticular substance, and this serves for origin and insertion of the muscles.

Fig. 8 (Pl. 29) shows the arrangement of the longitudinal muscles in the proboscis. As there is an outer circular layer, it follows that the longitudinal fibres must insinuate themselves between the fibres of this to be inserted in the basal membrane of the ectoderm. Besides these fibres there is a median plate of dorso-ventral muscles, which make up the main mass of the median septum separating the two ventral pockets of the proboscis cavity. These do not cease, however, at the dorsal edge of this septum, but are continued right to the mid-dorsal line. The interesting point, however, is that the antero-posterior extent of this plate is correlated to the length of the head of the notochord; hence the notochord in front of the skeletal rod appears to have a supporting function, and many of these fibres are, in fact, inserted in its basal membrane.

Fig. 9 shows the relation of the muscles of the anterior face of the collar region to the skeletal rod. Spengel has made some very interesting observations on the habits of Balanoglossus. From these it appears that the animal progresses by burying itself in the sand and passing the sand through its alimentary canal, and hence that locomotion and nutrition are effected by one and the same process. It further appears that it is the proboscis and collar which are the active agents in locomotion, the rest of the body being dragged passively behind. Hence we can understand why the muscular, nervous, and skeletal systems should be so highly developed in the anterior part of the body, and also why the animal should be

able to support with so little inconvenience serious truncations of its posterior end. A further interesting point is that neither proboscis nor collar is able to function unless it is turgid, and that it is impossible for it to attain this turgidity even when placed on a moist substratum if it is out of water. Hence it is probable that water is taken in through the proboscis and collar pores to set up this turgidity. This strikingly recalls a point in Echinoderm physiology. The only function which it is possible now to ascribe to the stone canal and madreporic pores, in view of the fact that the current in them is inwards,[1] is the maintenance of the turgidity of the water-vascular system.

The fact that the currents through the proboscis pore and the collar pores probably set inwards is not, as Professor Spengel points out, irreconcilable with the fact observed by Bateson, that carmine introduced into the proboscis cavity is ejected by the pore, since the contraction of the muscular wall on the fluid contents must necessarily cause ejection of the latter, together with any particles of an excretory nature which they may contain.

Fig. 9 shows us how the muscles of the anterior face of collar radiate from the skeletal rod, the more ventral fibres forming loops. The somatic wall of the collar cavity has an outer layer of circular muscles only on its anterior half; its muscles are mainly longitudinal. The splanchnic wall has an inner layer of longitudinal muscles. In the more primitive species these are gathered in front into a single bundle and inserted in the divergent crura of the skeletal rod; in other species only the more dorsal have this insertion. The circular muscles of the splanchnic wall are derived from a forward diverticulum of the trunk cœlom, which Spengel calls the peripharyngeal cavity. There is one on each side of the buccal cavity, and their relations to each other and to the perihæmal cavities are shown in figs. 4 and 10 (*P. Ph.*).

The chief point to notice in the trunk muscular system is

[1] Ludwig, H., "Uber die Function der Madreporenplatte der Echinodermen," 'Zool. Anzeiger,' No. 339, 1890.

the interruption of the somatic muscular system along the mid-dorsal and ventral lines and two dorso-lateral lines, the "submedian" lines in which the gonads open, and in three of the four genera also the gill-sacs; in Ptychodera, however, the outer gill-pores are situated dorsally to this line.

Both trunk and collar cœloms are traversed by radiating muscular fibres, and in the trunk both dorsal and ventral mesenteries persist, though in the collar they are partially absorbed. As has been mentioned above, a specialised dermis is absent, but there is a framework of connective-tissue cells ramifying amongst the proboscis muscles, and clothing the radiating muscles of the collar and trunk.

Classification of the Species.

Pl. 30, figs. 2—7 are intended to give some idea of the range of variation in external form found in the species of Enteropneusta. The main points to be noticed are the genital ridges of Ptychodera, small and inconspicuous in P. minuta, large and hiding the whole branchial region in P. erythræa, the liver saccules of Ptychodera and Schizocardium, the excessively short collar region of Glandiceps, and the immensely long proboscis of Balanoglossus Kowalevskii.

Professor Spengel has described in all nineteen species, nine of which are new. As, however, eight of these are founded on the examination of single, more or less mutilated specimens, their specific value must remain for the present somewhat doubtful. The Enteropneusta have an almost cosmopolitan distribution. Specimens have been found in the Mediterranean, Atlantic shores of France, Channel Islands, Orkney Islands, White Sea, Japanese coast, eastern coast of United States, coast of Brazil, and coast of Peru.

Spengel divides them into four genera, viz. Ptychodera, Schizocardium, Glandiceps, and Balanoglossus, all of which appear to me to be well founded.

Ptychodera includes the oldest known Neapolitan species.

It is the most differentiated genus, and has the following characters:

The proboscis has the typical form, being about one and a half times as long as broad; the collar is as long as it is broad, and the crura of the skeleton only reach through its anterior half.

The tongue-bars of the inner gill openings are bound to the sides of the sacs by synapticula, as shown in Pl. 29, fig. 13 *a*. We see that whereas in Amphioxus the synapticula run straight across the gill-slit, and are, according to Professor Spengel, secondarily fused with the tongue-bar, in Ptychodera they are at different levels on opposite sides of the tongue-bar.

The body in the branchio-genital region is produced into lateral flaps (Pl. 30, figs. 2 and 3), the genital wings, which contain a large portion of the gonads.

The digestive region of the gut is produced into papilla-like diverticula, which give rise to protrusions of the dorsal surface of the animal. These liver saccules are distinguished by the green matter which their cells contain; they open by narrow slits into the gut, and never contain food material.

In the branchio-genital region behind the gill-sacs we find the trunk cœlom divided into dorsal and ventral chambers by oblique septa. Each chamber contains a fork of the bifid gonad (see Pl. 29, fig. 11 *a*). These bifid gonads open along the line of insertion of this lateral septum. If we trace the septum backwards, it ends in a free edge at the commencement of the liver region; traced forwards towards the gill region, it becomes inserted on the skin at both ends; in other words, the dorsal chamber becomes displaced from the middle line by a median upgrowth of the ventral chamber, as shown in fig. 11 *b*. In the gill region the dorsal chamber becomes a small space containing no part of the gonad, and half choked with muscular and connective tissue (Fig. 5). From the fact that the dorsal chamber contains no radiating muscles, and that the lateral septum ends in free edge behind, but fuses com-

pletely with the skin in front, Professor Spengel concludes that the dorsal chamber is a forward diverticulum of the trunk cœlom behind the branchio-genital region.

The œsophagus is constricted into two tubes—a branchial tube above and a true œsophagus below—which are separated from each other by the apposition of two thickened ridges (fig. 14 *d*). The intestinal region of gut (behind the liver region) shows a lateral paired or unpaired groove with strong cilia. There is an external circular layer of muscles throughout the whole trunk, but the circular muscles of the proboscis are very thin.

The peripharyngeal cavities are of great extent, meeting each other in the mid-dorsal and mid-ventral lines; and since it is in the anterior walls of these cavities that the efferent vessels of the glomerulus run, it follows that in this genus they have a vertical course, and unite with each other to form a ventral collar plexus before opening into the ventral vessel of the trunk.

The central nervous system is connected with the dorsal epidermis by several dorsal roots. These latter have a sheath of nerve-fibrils, and hence there is a mantle of white matter on the dorsal as well as on the ventral and lateral surfaces of the cord. This genus contains nine species; the peculiarities of the more minutely investigated are mentioned below.

Pt. minuta (Plate 30, fig. 2) has very feeble genital ridges, into which the gonads send only rudimentary projections; 8—9 cm. long. Its collar skeleton is shown in fig. 8, and its central nervous system has the structure described in the introduction.

Pt. sarniensis, very similar, but much larger, about 50 cm. long. Central nervous system traversed by a single canal throughout, which, however, does not open into the posterior ectodermic sac.

Pt. aperta has great genital wings starting from immediately behind the collar, but not approaching each other; the

gonads send distinct branches into them. Central nervous system as in Pt. sarniensis.

Pt. clavigera, very large genital wings converging in front, so as to cover front part of gill region; the gonad branch which enters them is so large as to dwarf the ventral fork of the bifid gland from which it arises; central nervous system as in Pt. minuta.

Pt. aurantiaca, very like foregoing, but the still stronger genital wings contain, besides the great branch from the ventral fork of primary gonad, several longitudinal rows of accessory gonads with independent openings. Fig. 10 shows the form of its collar skeleton.

Pt. erythræa has immense genital wings, which completely hide the branchio-genital region, and extend in lesser development into front part of liver region. They, however, are not exactly equivalent to the genital wings of other species, since the lateral septa are inserted near their free edges. Hence they correspond chiefly to a comparatively narrow strip at the proximal end of the wings in other species. The outer gill-pores are elongated into vertical slits, and the ventral pocket of the proboscis cavity completely hollows out the "tooth" of the skeleton, converting it into a thin-walled sac.

Pt. bahamensis very closely resembles the foregoing species, but is very much smaller.

Spengel is inclined to divide this genus into three subgenera, viz. Ptychodera (sensu stricto), including Pt. minuta and sarmensis; Tauroglossus, including Pt. aperta, clavigera, aurantiaca; and Chlamydothorax, including Pt. erythæa and bahamensis.

The genus Schizocardium (fig. 7) was erected by Spengel for the reception of a common species of the Gulf of Rio de Janeiro, of which he obtained numerous specimens and made a very complete study. A second species of the same genus is founded on a fragment dredged up off the coast of Peru. It agrees with Ptychodera in possessing synapticula in the gill-skeleton, and liver saccules, but differs in

the entire absence of the lateral septum in the genital region, in the absence of genital wings, and especially in the structure of the central organs of the proboscis.

The notochord is prolonged as a narrow solid cord of cells almost to the anterior end of the proboscis; to this corresponds a prolongation of the plate of dorso-ventral muscles. The pericardium and heart are each prolonged into two great horns, which run alongside the notochord. It is from this circumstance that the name of the genus is derived. The mutual relation of these organs is shown by the series of sections represented in Pl. 29, figs. 12 *a*—*e*. The pericardium has lateral as well as ventral muscles, and the circular muscles of the proboscis are very strong.

The collar region has the skeletal rods reaching through two thirds of its length. There is a large mass of chondroid tissue easily distinguishable from the primary skeleton, and for this reason the collar skeleton (Pl. 30, figs. 11 and 13) is of clumsy build.

The central nervous system has no dorsal roots. The peripharyngeal cavities are confined to the lateral walls of the buccal cavity; hence their musculature is only dorso-ventral instead of circular: it is completed above by transverse muscles belonging to the ventral wall of the perihæmal cavities, and below by muscles derived from the collar cœlom; hence also there is no ventral collar blood-plexus, since the peripharyngeal cavities do not meet ventrally.

The inner gill-pores are so elongated as almost to meet in the mid-ventral line, leaving between them only (Pl. 29, fig. 14 *c*) a strip of hypobranchial epithelium. Though there are no genital wings like those of Ptychodera, yet the body is much broadened in the branchio-genital region, and these lateral portions contain several rows of gonads.

In the genital region there are a varying number of round pores opening from the gut to the exterior

somewhat dorsal to the submedian line—the line in which the gill-pores and gonads open in this genus. Of these, some just behind the gills are asymmetrically disposed; whilst separated from them by an interval, and placed just in front of the liver region are a pair.

There is no circular muscular layer in the trunk; it is replaced by a system of oblique dorso-ventral muscles arising from the dorsal mesentery, and ventro-dorsal arising from the ventral mesentery.

The genus Glandiceps is closely allied to Schizocardium. It includes two species—one from the deeper zone of the Mediterranean, another from the Bay of Tokio, in Japan; of the latter alone the whole body is known, and it will be taken as type.

Glandiceps differs from Schizocardium in the absence of synapticula in the gill-skeleton, and of liver saccules; also the pericardium has only two rudimentary anterior horns.

The proboscis resembles that of Glandiceps in the notochord and muscles. The collar region is extraordinarily short (Pl. 30, fig. 4), and the skeletal rods reach right to the end. The peripharyngeal cavities are entirely absent. The central nervous system has no roots. The inner gill-pores are not so long as in Schizocardium (Pl. 29, fig. 14 *b*). The genital region resembles that of Schizocardium; there are, however, additional gonads dorsal to gill-sacs, opening in the submedian line.

In the body musculature and gut-pores Glandiceps resembles Schizocardium. The chondroid tissue of the skeleton reaches its maximum of development in this genus; though there are no liver saccules, a liver region of the gut can be recognised by its histological characters, and in this region there is a dorsal siphon of non-glandular cells opening into the intestine before and behind.

The genus Balanoglossus includes several species differing widely from each other, but agreeing in the following characters:—The central organs of the proboscis are like

those of Ptychodera. The collar region is moderately long, and the skeletal rods reach right through it. They are consequently very long (Pl. 30, figs. 9 and 12). The inner gill-pores only reach halfway down the side of the œsophagus (fig. 14 *a*), but the lower nutritive portion is not constricted from the upper branchial. There are no synapticula in the gill-skeleton, and no liver saccules.

There is no circular muscular layer in the trunk, nor any system of muscles replacing it. The chondroid tissue is very feebly developed. The central nervous system has no dorsal roots.

B. Kupfferi (fig. 7) is the North Sea species. Its proboscis has the normal length. It has two proboscis pores opening into the right and left dorsal pockets of the proboscis cœlom. (In Ptychodera minuta this condition occurs as a variation; we also find one median pore opening into both pockets.) The head of the notochord is short; the neck has two lateral wings, giving rise to corresponding projections of the skeleton (Pl. 30, fig. 9 *W*). In full-grown animals the hinder part of the neck is broken up by invading portions of the skeleton. There are no peripharyngeal spaces, but there is a layer of circular muscles suspended in the midst of the collar cavity by the radiating muscles. There are, as in Glandiceps, additional dorsal gonads, and the eggs are large and yolky. There is a continuous blood-sinus round the whole gut behind the collar.

B. canadensis has a short round proboscis, in which the cavity is almost obsolete. The longitudinal muscles are represented by a septum of radiating muscles with interposed sheets of connective tissue. The head of the notochord has a wide lumen and a strong cuticular membrane, into which these muscles are inserted. The neck and the corresponding portion of the skeleton as well as its diverging crura are absent. There are two proboscis pores, but they are very narrow, and do not appear to reach the cavity. A sense-organ in the shape of a pit in the mid-ventral line of the proboscis is present.

There are no peripharyngeal spaces. There are four genital wings—a dorsal and a ventral pair—each with several rows of gonads, and they do not extend behind the gill region. The outer gill-pores are elongated to form slits extending between the dorsal and ventral wings.

B. Kowalevskii, the species the development of which has been worked out by Bateson, adheres very closely to the normal type. Its chief peculiarity is the enormous length of the proboscis (see fig. 6). The longitudinal muscles in this part are arranged in regular concentric layers. The notochord has a rather long head. Peripharyngeal spaces are present, and are obviously diverticula of the trunk cœlom, their walls containing not only circular but also longitudinal muscles. The lateral walls of collar are prolonged so as to cover three or four gill-slits (the so-called atrial folds). The central nervous system has no dorsal roots, but is connected with the dorsal epidermis by a longitudinal ridge of cells, such as is found in the young Ptychodera minuta. There are no dorsal gonads, but there are gut-pores, though only the more posterior paired pores are represented.

B. Mereschkovski is, as far as I can see, quite identical with B. Kowalevskii; B. sulcata has a similar proboscis, but its anatomy has not been investigated.

Balanoglossus Kowalevskii is in many respects the central form of the whole group; from it to Glandiceps the transition is not difficult, to which Schizocardium is also closely related. Unless we suppose synapticula to have been twice developed we must assume that the central organs of the proboscis of Ptychodera have undergone reduction, since the synapticula have evidently arisen between Glandiceps and Schizocardium.

Ontogeny.

The chapter on Ontogeny is exceedingly disappointing. Professor Spengel's observations have been confined to Tornariæ caught with the surface-net, and his methods appear to have been of a very crude nature. Though he has observed

the metamorphosis of the larva into the young worm, he has not seen the development of the notochord or central nervous system. His youngest larvæ had a complete gut with mouth and anus, and the proboscis cœlom opening already by its pore. He has shown that the muscle connecting the apical plate or brain with the proboscis cavity is really double, and that its sheath is continuous with the peritoneum of the proboscis cavity. Morgan,[1] in his last paper, which has appeared since the publication of the monograph, confirms this, and goes further; he finds that the anterior unpaired part of the muscle is an anterior prolongation of the proboscis cavity, and that the paired portions are formed from its lateral walls, and hence these muscles are strictly comparable to the muscles of the præoral lobe of Asterid larvæ. Thus one of the few resemblances to the trochosphere which Tornaria was supposed to exhibit is cancelled. The only important organ, the origin of which Spengel has satisfactorily determined, is the trunk cœlom, and here his results confirm those of Bateson. In reading his discussion of the morphology of Tornaria he gives one the impression that he has seen the origin of the collar cœlom. This is not so, as can be seen by a reference to the chapter on Ontogeny. He assumes that it is segmented off from the front end of the trunk cœlom, a supposition which is in contradiction to the results of both Bateson and Morgan.

He believes that he has seen the collar pore arising as an outgrowth of the first gill-sac. This view of its origin, which is maintained in opposition to that of Bateson, who regarded it as arising as a thickening of the skin on the posterior free edge of the collar, is founded on the examination of one specimen mounted whole. In his last paper Morgan figures sections showing that Bateson's view is perfectly right. He tells us that there is an ectodermic invagination giving rise to the collar pore at its upper end, and that both the first and the second gill-sacs open into it in the species he

[1] T. H. Morgan, "The Development of Balanoglossus," 'Journal of Morphology,' vol. ix.

examined. Spengel states also that he has proved that the pericardium originates from the dorsal ectoderm. Here again, however, his main proof is one thick section, and again his results have been contradicted by Morgan. It throws considerable light on the prejudice with which Spengel has approached the discussion of the results obtained by other workers, that on this meagre evidence, and the assumption that the intestine is a proctodæum, he should maintain as probable, not only the ectodermic origin of the pericardium, but also of all the other cœlomic cavities in the animal. His theory of their method of formation is illustrated in Pl. 29, fig. 7. He assumes because they are ciliated and separated by constrictions from the stomach that both œsophagus and intestine are of ectodermal origin. The trunk cœlom arises from the latter, and he supposes the collar cœlom to be segmented from it—a process which he compares to the segmentation of the mesodermic band of an Annelid. He supposes the proboscis cavity to arise as an ectodermal ingrowth, and that the pericardium is its fellow, in spite of the fact that the probocis cavity is (apart from the pore) a bilaterally symmetrical structure, and that the pericardium is a median one.

Bateson, without definitely committing himself, suggested as probable that the gonads were derived from the ectoderm. Spengel, by the examination of young adults, has shown that their connection with the ectoderm is secondary, and supposes that they are derived from mesenchyme cells. Morgan has proved them to originate, as in all other Cœlomata, from the peritoneum.

Affinities of Enteropneusta with Chordata.

We have now reached the section of the monograph dealing with Professor Spengel's views on the relationships of the Enteropneusta and the morphology of their organs. These views may be briefly summarised thus: he denies utterly their relationship to the Chordata, and suggests, instead, distant Annelid affinities.

I shall briefly recapitulate the arguments for the Chordate

affinities of Balanoglossus as put forward by Bateson, and then examine how Professor Spengel meets them. The Chordata are absolutely distinguished from all other Metazoa by three characteristics: (1) they have a dorsal central nervous system, separated from the skin by invagination and containing a central canal; (2) the anterior portion of the alimentary canal has paired gill-slits; (3) they have an endodermic rod, which has acquired a supporting function, and which is separated from the mid-dorsal gut-wall. All these structures are found in Balanoglossus;[1] they have been sought elsewhere throughout the whole animal kingdom in vain. In addition to this, certain structures found in Amphioxus alone are compared to some of the peculiar structures of Balanoglossus. These are (1) the paired anterior enteric diverticula of Amphioxus, the left of which opens by a pore to the exterior, compared to the proboscis and its pore in Balanoglossus; (2) the covering of the gill-slits by a pair of atrial folds, from the walls of which a pair of excretory pores (the atrio-cœlomic funnels of Lankester) are developed, compared to the "atria" of B. Kowalevskii and the collar pores; (3) the secondary gill-bars, compared to the tongue-bars of Balanoglossus; (4) the mouth adapted for digging in both instances. Whether any or all of this latter series of comparisons are valid is, however, of minor importance; the theory of the Chordate affinities of the Enteropneusta stands or falls with the validity of the comparison between nerve-cord, notochord, and gill-slits of Amphioxus, and the structures bearing the same name in Balanoglossus.

With regard to the central nervous system, Professor Spengel maintains that it is only the part of the dorsal nerve-cord which belongs to the collar region; that it is found in the Tornaria as merely a part of this, the ventral nerve-cord being developed at the same time; and that the process of invagina-

[1] Throughout this discussion I use the name Balanoglossus as a general term, applicable to all the species of Enteropneusta, and do not in any way restrict its application to Spengel's genus so named.

tion has nothing to do with its formation, but only with its removal from the surface, since nervous matter is only found on its ventral and lateral surfaces. In adducing such considerations as in any way telling against its similarity to the nerve-cord of the Chordata, Professor Spengel betrays his hazy conceptions of Vertebrate embryology. The nerve-cord of Amphioxus, like that of Balanoglossus, appears as a median differentiated strip of ectoderm before any invagination commences; and so marked features do the ventral position of the white matter and the presence of numbers of non-nervous cells in the cord form in the developing lower Vertebrata, that one investigator has put forward the startling suggestion that the nerve-cord of Vertebrates represents the alimentary canal of Arthropoda with which the ventral nerve-cords have fused. That the collar-cord is really the central nervous system appears from Professor Spengel's account of its anatomy; it is no argument against this to say, as he does, that though ganglion-cells are more abundant in it, yet they occur sparsely in the trunk and dorsal and ventral cords. A similar mode of reasoning would prove that the nerve-ring and radial cords of Echinoderms are not central organs.

Professor Spengel's objections to regarding the organ which Bateson calls the notochord as homologous to the notochord of Vertebrata are of two kinds, histological and topographical. We shall deal with the former first.

Bateson stated that the head of the notochord was solid, and that its tissue was remarkably like that of the notochord of a young Elasmobranch. Spengel maintains that there is a narrow lumen throughout, though sometimes interrupted; and though there is a superficial resemblance in transverse section to notochordal tissue, yet it is only superficial, for the cells are epithelial cells, modified by the development of huge vacuoles, whereas he says true notochordal tissue consists of spherical cells more or less flattened against each other with vacuoles, and in the chinks between the spheres a gelatinous substance. This kind of tissue he thinks it im-

possible to conceive of as originating from epithelium. Here again we are astonished by Professor Spengel's strange ideas about Vertebrate ontogeny. In Amphioxus the notochord is a mid-dorsal strip of hypoblastic epithelium constricted off by the meeting of lateral grooves, exactly in the same manner as the hinder part of the notochord is formed in Balanoglossus. Further, according to Balfour,[1] the first changes which occur in it are the production of vacuoles in the cells and the formation of a cuticular sheath, exactly comparable to the thickened "border membrane" (Grenzmembran) in Balanoglossus. Spengel says that there is no evidence of the formation of skeletal products from this membrane in Vertebrata. The answer to this is that the greater part of the thick notochordal sheath in Amia is formed from the thickening of this membrane, and that, indeed, it is only in virtue of possessing such a firm membrane that a mass of vacuolated cells can function as a supporting structure at all. The later changes which occur in the notochord of Amphioxus, viz. the interposition of discs of cuticular substance between the cells, are not without parallel in some species of Enteropneusta. In Balanoglossus Kupfferi the lumen of the neck is occluded and its tissue broken into pieces by invading masses of cuticular substance. We can, I think, go even further, and maintain that in the chondroid tissue we have the first trace of a mesoblastic sheath. Spengel maintains that this tissue is fundamentally different from cartilage, since in the latter the cells are derived from a solid blastema, whereas in the former we have a number of solid cellular outgrowths from the cœlomic wall. This appears to me to be a difference of detail rather than of principle, more especially as Hatschek[1] has shown that the solid sclerotome of the Elasmobranch embryo is represented by a hollow diverticulum in the larva of Amphioxus. Figs. 1 *a*, *b*, and *c* in Pl. 30 are designed to show that the arrangement found in Balanoglossus is to some extent

[1] 'Text-book of Comparative Embryology,' vol. ii.

[2] Hatschek, "Ueber den Schichtenbau von Amphioxus," 'Anat. Anz.,' 1888.

intermediate between those observed in Amphioxus and the Elasmobranch embryo. Ch^1. denotes the primary cuticular sheath of the notochord, Ch^2. the mesoblast concerned in the formation of chondroid tissue, "membrana reuniens," and cartilage, in Balanoglossus, Amphioxus, and Scyllium respectively. The actual skeletal substance is indicated by dotting. We see that whereas in Amphioxus the sclerotome is a single hollow outgrowth on each side, in Balanoglossus it is represented by a number of more or less solid outgrowths, and in Scyllium by a single solid one.

Spengel's *topographical* arguments are (1) that the so-called notochord appears late in development; (2) that it shows no relation to the blastopore or its line of closure, such as has been described in Elasmobranchs; and (3) that it is on the ventral side of the dorsal vessel. The circumstance that the notochord and other chordate features appear comparatively late in the development of the Enteropneusta is one of the most interesting features of the group. They are, as Professor Lankester has pointed out, the only members of the chordate phylum which take us into "prechordate" times, and give us some reliable indication of the direction in which to look for the ancestry of the Chordata. The reason for the precocious appearance of notochord and nerve-cord in Vertebrate development is the *hurrying over* of the earliest stages whilst the embryo is still within the egg-membrane. In the larva of *Balanoglossus Kowalevskii* the notochord, nerve-cord, and the first pair of gill-slits are present at or immediately after the time of hatching. A precisely similar instance of the precocious appearance of an organ in *embryonic* as opposed to *larval* development is afforded by the Vertebrate oviduct. This appears in the chick on the fifth day, but in the frog only after terrestrial life has commenced and the tail is being absorbed.

The appearance, in the development of Elasmobranch and other heavily yolked eggs, of the formation of the notochord and nerve-cord by the coalescence of the two lips of a slit, giving the impression that in ancestral forms both were paired

structures placed at the sides of a long slit-like blastopore, seems to me to be only one of those numerous distortions of development which yolk produces. Starting from a blastosphere with a differentiated endodermic pole, let us suppose that those cells which are destined in the gastrula to form the ventral wall of the gut become swollen up with yolky inclusions. Then the process of invagination will be asymmetrical; it will be modified to a growing of the cells which are to form the dorsal gut-wall over the yolky cells like a lip. A moment's thought will convince anyone that this cannot take place on a spherical surface without a simultaneous coalescence of the cells destined to form the right side with those destined to form the left.

The position of the notochord with reference to the dorsal vessel presents at first sight a serious obstacle to homologising it with the notochord of Vertebrates. A little reflection will convince us, however, that (1) when the Vertebrate notochord was not as yet fully separated from the gut, it could not possibly have been, as it is now, dorsal to the aorta; and that (2) since, as Professor Spengel points out, blood-vessels are merely blastocœlic spaces, there was very probably at that period of its evolution a blood-vessel between the notochord and dorsal ectoderm exactly where we find one in Balanoglossus. As the notochord became separated from the gut it would press on and obliterate the vessel above it. This has actually happened at one point in Balanoglossus, the heart and dorsal vessel being joined in the proboscis neck by only an exceedingly narrow chink.

As the dorsal vessel disappeared the ventral vessel would gain in importance, and so constitute the central contractile organ or heart. The chief point which Spengel adduces in favour of his theory of Annelid relationship is the structure of the blood system, and especially the direction of circulation. This latter, according to an old observation of Kowalevsky's, which, as far as I can gather, Professor Spengel has not confirmed, is forwards in the dorsal vessel, and backwards in the ventral, thus agreeing with the Annelid arrangement as against that found in Vertebrates. This fact Professor Spengel considers as

finally decisive against an assumption of chordate affinities. How little weight is really to be attached to it in the case of the Protochordata can be seen by considering the case of Tunicata, where the direction of the blood-flow is periodically reversed. This fact seems to have escaped Professor Spengel's memory.

The attempt to prove that the gill-slits of Balanoglossus and Amphioxus, in spite of their extraordinary similarity, are morphologically different structures, is exceedingly weak. The facts adduced against their homology in the two animals, viz. the more dorsal position of the gill-pores in the Enteropneusta—the presence of cœlom in the tongue-bar and its absence in the primary branchial septum in the one case, and the opposite arrangement in the other—the slightly different arrangements of the gill-skeleton, are all points of detail.

As a matter of fact, the gills of Balanoglossus are more typically Vertebrate in structure than those of Amphioxus, inasmuch as in the former case, as in all the higher Vertebrata, we have gill-pouches, whereas in Amphioxus we have merely slits. These latter obviously correspond not to the small external gill-pores, but to the internal gill-slits of Balanoglossus, the outer portions of the gill-sacs having atrophied in Amphioxus in consequence of the development of the atrial fold, just as in Teleostei the development of the operculum has had a similar effect. It is true that in many of the species of Enteropneusta these inner slits do not as nearly reach the middle line as they do in Amphioxus, but we trust no serious morphologist will ask us to consider this an important difference, more especially as in Schizocardium they nearly meet in the middle line.

The fundamental plan of the gill-skeleton is the same in Enteropneusta as in Amphioxus, as it may be considered to consist in both cases of a series of U-shaped rods. These, in the latter case, have all united to form a continuous lattice-work; the persistence of cœlom in the tongue-bars of

Balanoglossus renders this impossible, and so we have a series of isolated tridents.

Morgan has, in his last paper, made the exceedingly interesting observation that in the young adult a cœlomic space is found in the gill septum in the same position as it occurs in Amphioxus, viz. on the outer side of the skeleton; and that, further, the single skeletal rod found later here is represented, at this stage, by two distinct rods. That the synapticula have been independently acquired in each case I am quite prepared to believe, especially as they are absent in the more primitive species of Enteropneusta; but one of Professor Spengel's arguments on this point seems to me to be absurd, viz. that in the one case the synapticula carry blood-vessels, and in the other they do not. A similar argument would prove that the interfilamentar concrescences of the gills of Mytilus had nothing to do with those in the gills of Anodon.

Professor Spengel's statement that the synapticula in Amphioxus are segmented off from the endostyle must be received with great caution. He gives no adequate proof of it in his paper[1] to which he refers, and it involves such alarming conclusions with regard to the formation of the gill-slits, that it is safe to maintain a completely sceptical attitude towards it till further proof is adduced.

The blood-supply of the gills of the Enteropneusta is doubtless, as Professor Spengel points out, exceedingly different from the branchial vessels of a Vertebrate; but its differences depend entirely on its more primitive and undifferentiated character. It is, in fact, nothing more than a portion of the enteric plexus; indeed, the whole blood-system of Balanoglossus is the most undifferentiated one which could well be imagined, and it is perfectly easy to see how the Vertebrate or, indeed, any other arrangement could have been evolved from it.

As every one knows, the alternative theory of Vertebrate

[1] J. W. Spengel, "Beiträg zur Kenntniss der Kiemen des Amphioxus," 'Zool. Jahrbücher Abt. für Anat. und Ont.,' 1891.

descent is Dohrn's famous Annelid theory. The most striking and, indeed, almost the only point of similarity between Annelids and Vertebrates is the metameric repetition of many of their organs which both exhibit. Bateson, in criticising this, pointed out that whereas in Annelids this metamerism depends on the repetition of mesoblastic segments, in Vertebrates the repetitions of certain sets of organs have taken place independently of each other; the series of gill-sacs, for instance, bears no relation to the series of myomeres. Spengel has made the daring attempt to explain away this well-known fact. He says that the gill-slits of Amphioxus are at first in strict correspondence with the myomeres. Considering the fact that this remark can only by any possibility be applied to the first dozen slits, and that they even arise long after the complete ventral fusion of the myomeres, it is difficult to see why any weight should be attached to a chance correspondence between the first few slits and the myomeres adjacent to them. Spengel's only evidence for this correspondence, such as it is, consists in some figures of Amphioxus larvæ in Willey's paper,[1] and if Professor Spengel had taken the trouble to count the slits and myomeres instead of resting satisfied with a superficial examination of the figures, he would have seen that the correspondence on which he relies does not exist.[2]

Having thus seen that no valid objections to the homology of the nerve-chord, notochord, and gill-slits of Amphioxus with the similarly named structures in Balanoglossus have been brought forward, we are the less concerned to defend the other homologies put forward by Bateson. No one, we suppose, will deny that the "tongue-bars" are similar structures in both animals. The "digging" mouth is probably in each case an

[1] Arthur Willey, "The Later Larval Development of Amphioxus," 'Quart. Journ. Micr. Sci.,' 1891.

[2] Professor Lankester has kindly looked carefully into this matter for me, and he writes me that at the time when three gill-slits are present in the larva if one counts the club-shaped gland as a fourth and makes allowance for the obliquity of the myotomes, an apparent correspondence exists between the two sets of organs. Such are the dimensions to which Spengel's "strict metamerism" of the gill-slits reduce on examination.

independent adaptation to burrowing life, since it seems likely that the main stem of the chordate phylum retained a pelagic life; the highly developed sense-organs point in this direction. As to the homology of the atrial fold in Amphioxus with the posterior edge of the collar in Enteropneusta, so long as we are ignorant of the representative of the collar cœlom in Chordata, it must remain merely a tentative suggestion. Morgan's researches have, however, destroyed one of Professor Spengel's main objections to this comparison, viz. his assertion that the collar pore opens into the first gill-slit. With regard to the homology of the anterior enteric diverticulum of Amphioxus with the proboscis cavity, it is difficult to believe that Professor Spengel is serious when he says that the proboscis cavity is not asymmetrical, but only the proboscis pore, and on that ground objects to its comparison with the præoral cœlom of Amphioxus, more especially as, when speaking of the Tornaria, he suggests that the proboscis cavity is really a left-sided structure, the fellow of which is the pericardium.

Affinities of Enteropneusta with Annelida.

As mentioned above, Professor Spengel believes that Balanoglossus is distantly related to the Annnelida; and in support of this view he endeavours to show that the Tornaria is a modified trochosphere. Now Tornaria shows very great resemblance to an Echinoderm larva, so that it was for a long time mistaken for one; the only points in which it agrees with the trophosphere, and differs from all Echinoderm larvæ, are the possession of eye-spots on its apical plate, and the strong muscles running from the plate to the œsophagus. These latter, however, since they are merely differentiations of the præoral cœlomic wall, may be compared to the longitudinal muscles in the præoral lobe of Bipinnaria. Hence in order to torture the Tornaria into a trochosphere, he finds it necessary to make a series of violent assumptions, which are not only not supported by observations, but in direct contradiction to such observations as we have. In this connection, also, it is impossible to avoid expressing indignation at the way in which the results of the

careful investigations of Bateson are set aside when they do not happen to tally with Professor Spengel's theories. Bateson's researches established the following points of resemblance between the development of the larva he investigated and that of Echinoderms. (1) The blastopore closes in the position of the future anus. (2) The entire alimentary canal from mouth to anus is of endodermic origin. (3) The mesoderm originates as archenteric diverticula. In the trochosphere, on the other hand, the blastopore when it persists becomes the mouth, there is a stomodæum and a proctodæum, and the mesoblast originates by budding from two large cells in the neighbourhood of the blastopore.

Now Spengel says with regard to the first of these differences, "I cannot put it otherwise, in spite of Bateson's researches, than that we are still ignorant of the earlier stages of development;" and "Bateson's statements as to the blastopore do not appear to me to be more trustworthy than those of others who have observed the persistence of the blastopore as anus in other animals." Bateson's figures, however, give demonstrative proof that his statement is correct. The Tornaria larva has, as we know, a longitudinal ciliated post-oral band, and behind this a perianal one. Now in Bateson's larva this perianal band is the only one present, and it appears very early. In one of his figures we see it appear on an almost spherical gastrula and in the centre of it we see the disappearing blastopore. What further proof Professor Spengel would desire is not quite clear to me. With regard to the absence of stomodæum and proctodæum, he says, "In the absence of figures it is impossible to form any opinion as to the value of Bateson's statements." Now the mouth and anus do not appear till after gill slits and notochord have been formed, and to demand figures before accepting results about which it is difficult to imagine that a worker who used modern methods, like Bateson, could be mistaken, only exhibits the amount of prejudice which has clouded Professor Spengel's mental vision.

With regard to the origin of the cœlomic cavities as endodermic pouches, Spengel complains that the transverse

sections showing this are all taken from a single series; that in the case of the proboscis cavity the transverse section only shows a constriction of the gut; and that in the single longitudinal section figured which shows the anterior cœlom opening into the archenteron, there is an abrupt break in the character of the cells; the gut-cells do not, he says, gradually pass into cœlomic cells, thus suggesting that the opening figured is an artefact. Now so little is the insinuation justified that Bateson founded his results on a single series, that he does not express complete certainty as to the original connection of the collar cœlom with the gut, because he found the openings of communication in "very few" of the larvæ. Does Professor Spengel mean to demand that a zoologist should figure all the sections he has obtained which show a certain point? I imagine that few editors of scientific journals would relish the prospect. His objection to the longitudinal section can be met with a direct denial; the section appears to any one accustomed to the appearances presented by the developing cœlom of Echinoderms to be perfectly normal, a transition from gut-cell to cœlomic cells can be made out. It is hardly needful to add that the constriction of an anterior cœlom from the gut, and a "constriction of the gut," are one and the same. To what miserably small dimensions the supposed "trochophoral" peculiarities of the Tornaria reduce on examination we have shown above; that the principal ciliated ring of the trochosphere, the prototroch, is not represented in Tornaria, Spengel himself has admitted. The absence of those most characteristic organs of the trochosphere, the head kidneys, he regards as of little importance, as also the presence of a præoral cœlom totally unrepresented in the trochosphere. His calm assumption, in defiance of evidence to the contrary, that the œsophagus and intestine are of ectodermal origin, I have dealt with above. In this connection also it should be remarked that he mistakenly attributes to Professor Huxley the terms stomodæum and proctodæum, which we owe to Professor Lankester.

In justice, however, to Professor Spengel, we ought to add

that he does not appear to have convinced himself of the truth of his own theory, because in discussing possible affinities of the Enteropneusta with the Echinoderms, he admits that there is a strong resemblance between the larvæ, and proceeds even to suggest homologies. He believes that the collar pores may correspond to the two madreporic pores which have been observed in the larva of Asterias by Field.[1] Here again, however, Professor Spengel's imperfect understanding of what has been done in other groups has misled him. Neither Bury[2] nor Field has, as he imagines, described a transitory right hydrocœle. Bury distinctly states that he regards the hydrocœle as a structure which has been from the first unpaired; he does describe a right anterior cœlom as well as a left, but the left anterior cœlom is not the hydrocœle. The oldest larva described by Field did not show a trace of the hydrocœle, though some of the younger possessed two madreporic pores; but it is now a dozen years since Ludwig[3] proved that the madreporic pore primarily opens into the cœlom, and that its connection with the hydrocœle is secondary. The most interesting feature of Enteropneustan development is the strong resemblance to the Echinoderm larva which Tornaria presents, which renders at least plausible the suggestion that the Protochordata and the Echinoderms diverged from a common bilaterally symmetrical pelagic ancestor. On what other grounds besides the illusory resemblances of their larvæ does Spengel ask us to base our belief on a distant affinity between Enteropneusta and Annelids? On the assertion that the collar cœlom is segmented from the trunk cœlom, like a mesoblastic somite from the germinal band of Annelids (this, as I have already said, is an assumption contradicted by both Bateson and Morgan), and on the direction of circulation in the dorsal and ventral vessels. It is surely not going too far to say that a zoologist who

[1] Field, "The Larva of Asterias," 'Quart. Journ. Micr. Sci.,' 1892.

[2] H. Bury, "Studies in the Embryology of Echinoderms," 'Quart. Journ. Micr. Sci.,' 1889.

[3] Ludwig, "Entwickelungsgeschichte der Asterina gibbosa," 'Zeit. für wiss Zoologie,' Bd. xxxvii.

explains away the striking Chordate features presented by gill-sacs and nerve-cord, and founds a new theory on such a basis as I have just mentioned, can hardly expect to have much weight attached to his judgment.

In conclusion I may be allowed to express my regret that Professor Spengel has not condensed his work more. The amount of apparently needless repetition is very great, which is all the more to be regretted as the amount of literature which every zoologist must read is immense and daily growing.

Those who believe in the Chordate affinities of Balanoglossus will, however, derive consolation from the fact that in the huge volume we have been considering, every possible argument has been urged against this theory, and that, notwithstanding the great industry and ability which Professor Spengel has displayed in attacking it, all his attempts to shake it have, in my mind, signally failed.

Zoological Laboratory, Cambridge;
May 3rd, 1894.

EXPLANATION OF PLATES 29 & 30,

Illustrating Mr. E. W. Macbride's Review of Professor Spengel's Monograph on Balanoglossus.

List of Abbreviations used.

Al. Alimentary canal. *Al. Br.* Dorsal branchial region of the alimentary canal. *Al. œ.* Ventral œsophageal region of the alimentary canal. *Br.* Branchial sac. *Br. in.*, *Br. ex.* Internal and external openings of the same. *Br. sk.* 1. Skeletal rod in primary gill-bar or gill-septum. *Br. sk.* 2. Skeletal rod in secondary gill-bar or "tongue-bar." *Bucc.* Buccal cavity or pharynx. *C.* Collar. *C. cœ.* Collar cœlom. *Ch.* Notochord. *Ch*[1]. Primary cuticular sheath of the same. *Ch*[2]. Secondary mesoblastic sheath of the same. *C. N.* Central nervous system. *C. p.* Collar-pore. *D. N.* Dorsal nerve-cord of trunk. *D. R.* Dorsal roots of central nervous system. *D. V.* Dorsal blood-vessel. *Ep.Br.* Epibranchial epithelial band. *Gl.* Glomerulus. *Gon.* Gonad.

Gen. R. Genital ridge. *Ht.* Heart. *Ht. aur.* Auricular prolongations of heart of Schizocardium. *Hy. Br.* Hypobranchial epithelial band of Schizocardium. *Li.* Liver saccules. *L. S.* Lateral septum of trunk cœlom. *M.* Mouth. *Musc.* Muscular fibres. *Mycœ.* Myocœle. *P. C.* Pericardium. *P. C. Aur.* Auricular prolongations of pericardium of Schizocardium. *P. E.* Perihæmal space. *Pph.* Peripharyngeal space. *Pr.* Proboscis. *Pr. Cœ.* Proboscis cœlom. *Pr. Cœ. V.* Ventral pocket of proboscis cœlom. *Pr. P.* Proboscis pore. *Pr. vm.* Ventral mesentery of proboscis cœlom. *Proct.* Proctodæum. *Scl.* Sclerotome. *Sp. Cœ.* Splanchnocœle. *Stom.* Stomodæum. *Sy.* Synapticulum. *T. B.* Tongue-bar. *Tr.* Trunk. *Tr. cœ. d.* Dorsal division of trunk cœlom. *Tr. cœ. v.* Ventral division of the same. *Tr. d. m.* Dorsal mesentery of trunk cœlom. *Tr. v. m.* Ventral mesentery of trunk cœlom. *V. N.* Ventral nerve-cord of trunk. *V. V.* Ventral blood-vessel.

PLATE 29.

Figs. 3, 4, and 5, and Figs. 8—14 inclusive, are taken from the monograph, though in some cases simplified in detail.

Figs. 2—13 inclusive are copied directly from the monograph.

(All figures diagrammatic.)

Fig. 1.—Horizontal longitudinal section of Balanoglossus.

Fig. 2.—Sagittal longitudinal section of Balanoglossus (Ptychodera).

Fig. 3.—Transverse section of proboscis region.

Fig. 4.—Transverse section of collar region.

Fig. 5.—Transverse section of branchiogenital region.

Fig. 6.—Horizontal longitudinal section of embryo of Balanoglossus Kowalevskii, according to Mr. Bateson.

Fig. 7.—Ideal sagittal section of developing Tornaria, illustrating Professor Spengel's theory of the formation of the mesoderm.

Fig. 8.—Illustrates arrangement of fibres in the longitudinal muscular layer of the proboscis.

Fig. 9.—Illustrates arrangement of fibres in the circular muscular layer of the anterior wall of the collar cavity.

Fig. 10.—Sagittal section of collar region, showing mutual relations of collar cœlom, trunk cœlom, perihæmal and peripharyngeal spaces.

Figs. 11*a*, 11*b*.—Transverse sections of trunk, showing insertion of lateral septum. Fig. 11*a* is behind the gill region; Fig. 11*b* is in the hinder part of the gill region.

Figs. 12*a*, *b*, *c*, *d*, *e*.—A series of five transverse sections through the anterior part of the notochord and adjacent pericardium and heart in Schizocardium.

FIG. 13*a*.—Diagram of two "inner gill-pores" of Balanoglossus (Ptychodera), showing their skeletal structures and the relation of the latter to the slits. *Br. sep.* Gill septum.

FIG. 13*b*.—Similar diagram of three complete gill-slits of Amphioxus. *Br. sl.* Gill-slits.

FIG. 14*a*.—Diagram showing the extent to which the gill-sacs are developed in a vertical direction in Balanoglossus (sensu stricto).

FIG. 14*b*.—Similar diagram of gills of glandiceps.

FIG. 14*c*.—Ditto, ditto, Schizocardium.

FIG. 14*d*.—Ditto, ditto, Ptychodera.

PLATE 30.

FIG. 1*a*.—Diagrammatic transverse section of Amphioxus larva, showing the division of cœlom into splanchnocœle and myocœle, the hollow sclerotome and its relation to the notochordal sheath.

FIG. 1*b*.—Similar section of Balanoglossus. *Ch*². The mesoblastic sheath of "chondroid tissue."

FIG. 1*c*.—Similar section of the Scyllium embryo. *Scl.* The sclerotome, here a solid outgrowth from the wall of the myocele.

FIG. 2.—Ptychodera minuta. Dorsal aspect. *G. p.* Outer gill-pores. Magnification $\frac{2}{1}$.

FIG. 3.—Ptychodera erythræa. Dorsal aspect. Natural size.

FIG. 4.—Glandiceps Lachsi. Dorsal aspect. Natural size.

FIG. 5.—Schizocardium brasiliense. From the side.

FIG. 6.—Balanoglossus Kowalevskii. Magnification $\frac{4}{1}$.

FIG. 7.—Balanoglossus Kupfferi. Natural size.

FIG. 8.—Collar skeleton of Ptychodera minuta.

FIG. 9.—Collar skeleton of Balanoglossus Kupfferi. *E.* Head. *W.* Wings. *B.* Body. *L.* Crura.

FIG. 10.—Collar skeleton of Ptychodera aurantiaca.

FIG. 11.—Collar skeleton of Schizocardium brasiliense.

FIG. 12.—Collar skeleton of Balanoglossus Kowalevskii.

FIG. 13.—Collar skeleton of Schizocardium peruvianum.

Notes on a Gregarine of the Earthworm (Lumbricus herculeus).

By

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With Plate 31.

While looking through some worms which had been obtained for dissection in Professor Ray Lankester's laboratory at Oxford, Dr. Benham, Senior Assistant to Professor Lankester, noticed one specimen the hinder end of which appeared to be filled with small white bodies easily visible through the body-wall of the worm. These were preserved by Mr. E. A. Minchin, who identified them as a species of Gregarina, and by whose kindness I was allowed to examine them. As they presented some points of interest, perhaps these few notes may not be out of place.

Previous Observations.—On referring to the literature of the subject, I found that this species of Gregarine had been before observed and described, as a very careful account of it appears in the well-known paper of Lieberkühn (1), who mentions Meckel as a still earlier observer of these creatures. Lieberkühn describes this Gregarine as occurring in great numbers in the body-cavity of the worm, especially towards the tail; as being round in shape and white in colour; and he gives some account of its conjugation, spores, &c., but does not name the species. A round Gregarine is also described by Schmidt (2) as occurring in Lumbricus olidus, but this is figured as possessing a shaggy cuticle, and therefore appears to

be a different species from the one occurring in L. herculeus, of which the following is a brief account.

Description, Habitat, &c.—The animal is of a pure white colour, and quite opaque. It is rounded in form, generally spherical, but some individuals are of a blunt oval shape (fig. 1); and others, again, apparently young specimens, appear as flattened oval discs. They vary in size from minute specks to bodies with a diameter of over 1 mm. An average specimen measured under the microscope gave the proportions 1·2 by ·9 mm. A few individuals occurred in the hinder segments of nearly all the worms (L. herculeus) which I opened. In one or two instances almost the whole body-cavity was filled with Gregarines. (In a number of specimens of Allolobophora fœtida (?) which I examined I did not find any of these animals.) They lie seemingly loose in the cœlom, but I have found young specimens embedded in a growth of cells along the intestine of the worm, and cysts very constantly in the same position (see p. 429).

Influences affecting Development.—Gregarines in different stages of development may apparently exist side by side in the same host, but in most cases there appeared a great preponderance of these in one condition, either as cysts, or conjugating pairs, or mature individuals, which fact would seem to point either to some external influence acting on the parasites, e.g. some alteration in the nature of their environment, leading them to a simultaneous change of state, or, as seems perhaps more probable, to a definite cycle in their lives in accordance with the seasons of the year—since I found mature Gregarines plentiful in the autumn and winter months, many instances of conjugation about the spring, while during the summer I could not find any specimens other than cysts and spores.

Evidence seems wanting as to whether the well-being of the host is affected by the presence of Gregarines. On the one hand, worms of the most healthy appearance contained a considerable number of the parasites, while, on the other, a very sickly and apparently moribund worm was crowded with

gregarines, all conjugating. Here it might be suggested that if the gregarines were the cause of the illness of their host, the state of health of the latter had in turn affected them, and that this preparation for the formation of spores on their part was in view of the imminent death of the worm, the destruction of their home and their own dispersion over the soil,—to be taken in perhaps as falciform bodies in the earth swallowed by other worms, and so to find another habitation.

I have not been able to observe any movement in these gregarines, nor does their circular form seem adapted to progression.

Microscopical Details.—Cuticle.—Coming to microscopical details, little need be said about the cuticle. It is, as described in other gregarines, very elastic, of a granular appearance, presenting in sections a distinct double contour. It dissolves rather slowly in strong acids, more rapidly in potash, but in each case becomes so transparent before dissolving that its actual disappearance is difficult to follow.

Paraglycogen Granules.—In a teased specimen the bulk of the animal appeared to consist of round granules of various sizes, colourless or of a faint greenish colour by transmitted light. They appeared quite circular, and the largest measured as much as 15 μ in diameter. In those Gregarines which I first examined and which had been preserved in alcohol the granules presented a very curious appearance, many of them containing what looked like a crystal in the form of a three- or four-pointed star (fig. 3, *b. c.*). The same was seen in stained sections, the apparent crystal being even more marked and seeming in double-stained preparations to take a different colour from the rest of the granule. The granules from a fresh specimen were quite homogeneous, so that it was evident that the crystal, if such it really were, was produced by the reagents used in hardening. Experiments tried on the fresh granules gave the following results:—The addition of absolute alcohol and then of benzol produced at first no apparent result; on washing out the benzol, however, with alcohol the star-like appearance was produced, and on again adding benzol

a more marked variety—an apparently more massive crystal—was seen. Washing out the benzol once more and then adding water caused the crystalline appearance to vanish almost entirely, a faint semblance of crossing lines in the substance of the granule being all that was left visible (fig. 3, *b. c. d.*), while this substance itself first became opaque and then cleared again. The re-addition of the former reagents caused the reappearance of the crystals. Oil of cloves similarly used seemed even more effectual in their production than benzol. What the nature of the phenomenon may be is difficult to say. It may be that true crystals are formed, modified by their organic origin and surroundings, being precipitated from alcohol and benzol and redissolved in water. On the other hand, it may be suggested that such an appearance could be produced by a splitting of the substance of the granule in consequence of a shrinkage caused by the reagents. This explanation seems perhaps to harmonise better with the phenomenon of the faint lines left on the disappearance of the crystal in water, i.e. a line of division remained to mark the original cleft; also in many cases where the granules appeared split into two halves the line of cleavage corresponded very closely with the dark lines forming the limbs of the stars (fig. 3 *g*, *h*), which lines seemed in some instances to extend from edge to edge of the granule. Further, in one case at least I thought I could detect a forking of the end of one of the radiating lines which would not be possible in a crystal, and in one instance when the objective was accidentally screwed down so as to touch the cover-glass and crush the section beneath, the flattening of the granules was accompanied by entire disappearance of the "crystals." This explanation (viz. as hollows in the granules) is given by Wolters (3) of the rather different crystalline appearance seen by him in another gregarine, but the apparent staining of the "crystals" in some preparations seems a difficulty in the way of this explanation.[1] The same

[1] Actual crystals were found by Frenzel (4) in other Gregarines, but these appear to occur not in, but among the granules. Might not these crystals be comparable to the crystals found in plants, which apparently are excretory products?

observer also suggests that the granules are a supply of food-substance for the gregarine, used up when necessary, in reference to which view I may mention that in a teased specimen containing chiefly sporoblasts, among which were a few granules, the latter appeared oval or irregular in shape, as if undergoing a process of corrosion and absorption.

The granules gave the usual paraglycogen reaction with iodine and sulphuric acid, swelling up in the strong acid in a very curious manner, with a distinctly double-contoured appearance, and finally dissolving (fig. 3 *i*). They dissolved rapidly and entirely in potash, even when diluted to 1 per cent. In many preparations the granules appeared to form the whole substance of the animal (fig. 2), but in others a certain amount of formless protoplasm was visible among them, and no doubt this is really present in all cases. It was well shown in a preparation stained with gentian violet and orange, the protoplasm taking the latter colour, the granules the former. In many cases sections showed a number of deeply-staining spots among the granules, as if the protoplasm had collected together into nodes; and in one series a distinct network was visible (fig. 4), due no doubt, as Wolters holds, to the action of reagents.

Capsule.—The question of the amount of protoplasm existing in the gregarine beside the paraglycogen granules seems intimately connected with a curious appearance seen in the greater part of the series of sections of mature gregarines which I cut; this was a ring of staining substance which went through as many as sixteen sections of 5 μ thickness, gradually contracting and disappearing. It was therefore a hollow sphere, and it contained within itself matter in no respect differing from the rest of the animal's body (figs. 2 *a*, 2 *b*). It did not present any sharply-defined outline, such as would suggest a containing-membrane, but appeared rather to be a continuous "capsule" of protoplasm within the gregarine, which was in some cases centrally, in others eccentrically placed. It seems possible that the appearance may be caused by the reagents employed driving the fluid protoplasm before them from the sides inwards as they penetrate, thus forming a ring,

or, as it rather appeared in some cases, a lump of protoplasm towards the centre, with the granules which were originally there appearing in the midst of it. This explanation was suggested by Professor Lankester in the case of a somewhat similar appearance found by Miss L. J. Gould (5) in Pelomyxa. However, in one instance there appeared to be two such formations in the same animal (fig. 5) ; in another, the whole central portion of the gregarine formed a distinct round mass, staining more darkly than the rest of the substance and divided off from it by a dark line, as to the nature of which—whether it were a definite membrane or not—I was exceedingly doubtful (fig. 6). Mr. Minchin suggests that the phenomenon is rather to be regarded as a preliminary to the stage of spore-formation, and it was he who applied to it the name "capsule," which I have used. But its nature must for the present remain obscure.

Nucleus.—The nucleus in a teased fresh specimen appeared perfectly spherical, about 70 μ in diameter, with a circular nucleolus dimly visible. It was quite colourless and transparent (fig. 7). In the process of hardening it invariably shrank, and in sections was always much crumpled. It was bounded by a membrane, which appeared double-contoured under a high power. The ground-substance was finely granular in appearance, and it contained as a rule two nucleoli, but sometimes more—in one instance as many as five (figs. 8, 9). The nucleoli were highly vacuolated, the vacuoles in some instances seeming to have some contents capable of being stained (fig. 10).

Life History.—The following is a brief account of those stages in the development of this gregarine which I have been able to observe:

Conjugation.—Conjugation first takes place, two round individuals becoming pressed and flattened one against the other, the cuticles of the two coalescing at the portions where they are applied one to the other. I have not been able to observe any mitosis in the nuclei, but in those cases in which the conjugating gregarines each contained a single undivided

nucleus the structure of this was peculiar, almost all the contents of the nuclear membrane being gathered into a single large mass, situated at one side (fig. 11). This is no doubt preparatory to division, which probably takes place with mitosis as described by Wolters in other Gregarines. The next stage which I have myself seen is one in which the nucleus has broken up into minute portions, of about the same size as the larger paraglycogen granules; these fragments are scattered pretty evenly throughout the body of the animal, and are very inconspicuous. They were pointed out to me by Mr. Minchin, who kindly examined some of my preparations, and when once demonstrated were fairly easily seen, as in a preparation stained with hæmatoxylin and eosin they were dyed a distinctly bluer colour than the surrounding granules (fig. 12). I did not see any breach of continuity in the septum formed by the coalesced cuticles which separates the conjugating Gregarines, through which any interchange of substance might occur; nor have I seen the nuclei or nuclear fragments apparently attracted towards one another in this species. In a specimen of Monocystis agilis, from one of the vesiculæ seminales of the worm, the nuclei of the two conjugating individuals were drawn together to the opposite sides of the septum (fig. 21), and probably the latter is ultimately entirely absorbed, as it does not appear in cysts containing spores.

Sporoblastomeres and Sporoblasts.—The next stage is the formation of sporoblastomeres (Minchin) by the separation of the substance of the animal into masses, each surrounding a fragment of the nucleus. These appeared in fresh preparations to be surrounded by a transparent coat, but this is either not universally the case, or disappears in permanent preparations (figs. 13 *a*, *b*). In some the original granules still appear embedded; at a later stage these disappear, and the masses become homogeneous; they are of different sizes, and contain one or more nuclei (fig. 13*b*). I have found specimens containing one, two, and four nuclei, suggesting a tetraschistic division into the ultimate sporoblasts. These latter become elongated and boat-shaped before secret-

ing their spore-coat (fig. 14). The nucleus is placed almost invariably to one side, on the equator of the sporoblast.

Spores and Falciform Bodies.—The formation of spores from the sporoblasts appears to begin at the outside of the cyst, and in one preparation the spores seemed to be so arranged as to point outwards, with their long axis on the radii of the cyst (fig. 15), the centre being occupied by sporoblastomeres. In many cases a number of granules remain unabsorbed till the end. It may be noted that the characteristic knobs at the end of the spores seem to disappear entirely in permanent preparations, either dissolving in the reagents or becoming invisible owing to their possessing an index of refraction equal to that of Canada balsam. In glycerine these processes were still visible. In two cases out of a large number of cysts examined I have seen a specimen of the curious triangular spores figured by Lieberkuhn, which are probably monstrosities. The development of the spores proceeds as follows:—The nucleus divides into two, then each fragment divides again, and the four resulting fragments divide once more. There are thus formed eight small round nuclei, lying in the protoplasm of the spore (fig. 16). The exact process of division, with or without mitosis, I have not been able to follow. The protoplasm surrounding these nuclear fragments divides, and a portion surrounds each, these portions elongating and forming the falciform bodies. The nucleus in these lies almost at the extreme end (fig. 17). The arrangement of the falciform bodies in the spore does not appear to be constant, the most favourite being perhaps that in which the nuclei or heads lie towards the centre, the tails pointing four to either end of the spore (fig. 17 *b*). The falciform bodies are coloured very prettily by the Ehrlich-Biondi stain; the nuclei appearing green, the body pink.[1] Their shape seems to vary considerably, some being longer, others thicker; but it is possible that these differences represent stages in their elongation and development.

[1] In the mature Gregarines the nucleoli were stained a bright pink by this reagent, the ground-substance of the nucleus taking the same colour, but very faintly.

Position of Gregarines in the Worm.—A few more points remain to be noted. With regard to the position in the worm of the Gregarines at various stages, it may be mentioned that the adult gregarines and the cysts which I first found, also the conjugating pairs, lay in the cœlom of the worm, as before stated; later on, in the summer, I had great difficulty in finding any in this position, but discovered that the cysts were to be found embedded in certain oval or sausage-shaped masses of tissue, which appeared to lie loose, or but slightly attached, beneath the gut in the hinder segments of the worm. These masses seemed to consist of altered and degenerated nephridia, and were in some cases composed entirely of cells, in others of an apparently structureless matrix, with a few cells here and there (fig. 18). The Gregarines occurred in them along with a number of encysted nematodes, so that it was impossible to say whether the growth in which they lay was due to the latter or to the gregarines; but Dr. Benham assured me that the formation was certainly abnormal in the worm.[1] If the Gregarines were the cause of this growth, the fact might have a pathological interest, in view of the suggestion that some cancerous tumours are caused by a psorosperm, as is the case in the disease peculiar to rabbits caused by Coccidium oviforme. The sausage-shaped growths in the worm were in some cases honeycombed with cysts of small size closely packed together (fig. 18); in other cases only a few larger cysts occurred in each. In one or two specimens of mature Gregarines, which I found apparently loose in the cœlom, there were a certain number of tissue-cells attached to the cuticle, showing either that it had once been embedded in a similar growth, or rather perhaps that it was about to embed itself, but interrupted before the process had proceeded far. The suggestion that the falciform bodies make their way out of the worm to find another

[1] Metchnikoff (6) records that the gregarine-cysts in the vesiculæ seminales become surrounded by a mass of phagocytes which attack and sometimes succeed in killing them. The masses of cells above described seem also to be of an inflammatory nature, but it seems doubtful whether they injure the enclosed cyst, in which I have not noticed any marked signs of degeneration.

host seems all the more likely from the fact that the cysts occur in the same masses of tissue as the nematodes, which are known to act in this manner.

Spores of two Sizes.—It is also of interest to note that there appear to be two different kinds of spores occurring in similar positions in cysts which are also similar, one being a large variety measuring approximately 30 μ in length by 12 μ in breadth, while the other is almost exactly half this size, viz. about 15 μ by 5 μ (fig. 19). The description of spore-development given above applies in the main to the larger variety which are more easily observed, but, as far as I have been able to make out, in the case of the smaller kind very similar changes occur. The size of individual cysts differs considerably in both kinds, but the cysts containing the smaller spores are not themselves necessarily smaller than those in which the large variety is found. I have found in one or two instances a cyst containing large spores surrounded by tissue, in which were embedded, apparently loose, a number of the smaller kind. In cutting some sections through portions of the vesiculæ seminales of a worm, I also found cysts containing spores of two different sizes, corresponding very closely with the two varieties found in the hinder end of the worm. It would be natural to suggest that these two varieties in the vesiculæ are respectively the spores of Monocystis magna and agilis, and that the spores in the posterior segments may also belong to these gregarines, the large round gregarines described being a form of M. magna. Against this theory, however, stands not only the distance from the known haunts of M. magna and agilis, but also the large size of the cysts of small spores, which could hardly be formed by M. agilis, while the cysts in the vesiculæ containing large spores were themselves no larger than those containing small ones; and it seems necessary to suppose, in default of further evidence, either that two sorts of spores are formed by each gregarine, or that still another species of gregarine remains to be described. It therefore appears best for the present to consider the round gregarine of the tail segments as distinct from the other

gregarines of the earthworm, and I would propose for it the name Monocystis herculea, on account of its large size and its occurring in Lumbricus herculeus.

As to the exact stage of development represented in fig. 20 I am still in doubt. Small round or oval bodies with one or more nuclei such as are there depicted occurred in a small number of cysts which were embedded, generally filling the whole cyst, though in the case figured they formed a sort of chain lying across it, apparently contained in a special membrane. It seems most probable that they are the sporoblastomeres of the smaller variety of spores, as from their containing more than one nucleus they can hardly be the final sporoblasts, and they are considerably smaller than the sporoblasts shown in fig. 14. On the other hand, they rather closely resemble the contents of the spores (fig. 16) where the nucleus is dividing, but they have no trace of any coat.

I may perhaps note in conclusion that whereas in the round gregarine described in this paper at the time of conjugation two spherical individuals become pressed and flattened against one another, in the specimens which I have seen of Monocystis magna the two gregarines lie side by side at length (fig. 21), and do not become circular as I understand Wolters to state.

It remains only for me to offer my most sincere thanks to Mr. Minchin for his continual kindness and assistance throughout the time during which I have been working at this subject. To him are entirely due any merits which this paper may possess. I must also thank Professor Ray Lankester for kindly allowing me the use of his laboratory, and Dr. Benham for many hints and suggestions from time to time.

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EXPLANATION OF PLATE 31,

Illustrating Mr. Wm. Cecil Bosanquet's paper, "Notes on a Gregarine of the Earthworm (Lumbricus herculeus)."

Fig. 1.—Mature gregarines and conjugating pairs, enlarged about four times.

Fig. 2 *a*.—Section of a mature gregarine, showing nucleus and capsule. × about 90.

Fig. 2 *b*.—Portion of the same section, showing capsule. × 280.

Fig. 3.—Various granules, showing the action of reagents. *a*. Granule seen fresh in normal saline. *b*. *c*. After addition of alcohol and benzol. *d*. On subsequent addition of water. *e*. *f*. Same granule in different focus, showing central spot dark and light respectively. *g*. *h*. Split granules. *i*. Granule swollen by sulphuric acid. × about 480.

Fig. 4.—Portion of substance of gregarine, showing apparent network of protoplasm. × about 300.

Fig. 5.—Portion of gregarine, showing two capsules. × 110.

Fig. 6.—Portion of gregarine, showing central mass divided off from the rest. × 110.

Fig. 7.—Nucleus in fresh teased preparation. × 300.

Fig. 8.—Nucleus (crumpled), showing two vacuolated nucleoli. × 600.

Fig. 9.—Nucleus with five nucleoli. × 700.

Fig. 10.—Nucleus and nucleolus, showing staining substance in the vacuole. × 600.

Fig. 11.—Nucleus at time of conjugation. × 450.

Fig. 12.—Nuclear fragments among granules, previous to formation of sporoblastomeres. Zeiss, homog. immers., 2 mm., oc. 4.

Fig. 13 *a*.—Sporoblastomeres, fresh, showing coat. × 450.

Fig. 13 *b*.—Sporoblastomeres, showing division of nucleus and granules embedded. From a permanent preparation in which the coats are not seen. × 450.

Fig. 14.—Sporoblasts. × 720.

Fig. 15.—Spores in cyst, showing arrangement (semi-diagrammatic). × about 100.

Fig. 16.—Spores in section, showing development of falciform bodies by division of nucleus. × 400.

Figs. 17 *a*, *b*.—Falciform bodies in spore. Sections of spores, showing only half the number. Crouch, homog. immers. $\frac{1}{12}$, oc. 2. × 800.

Fig. 18.—Portion of growth of cells surrounding the cysts. × 100.

Fig. 19.—Spores of two sizes. × 1000.

Fig. 20.—Doubtful stage, ? sporoblastomeres of small spores. × 700.

Fig. 21.—Conjugation of Monocystis agilis, showing mutual attraction of nuclei. × 420.

Fig. 22.—Conjugation of Monocystis magna. × 16.

Some Abnormal Annelids.

By

E. A. Andrews.

With Plates 32—34.

Amongst the Annelida, as amongst other groups of non-Vertebrates, various abnormalities and monstrosities may be found upon examining large numbers of individuals. Thus in some groups, as in the Eunicidæ, double and supernumerary antennæ and parapodia are not so very unusual, though they have received little or no attention as yet. Again, more fundamental abnormalities affecting the integrity of the body somites occur in widely separated groups of Annelids, as has been recently demonstrated by C. J. Cori, T. H. Morgan, and F. Buchanan. Even repetitions of considerable regions of the body, bifurcations of the main axis that produce a double monster have been observed again and again. As naturally to be expected from the accessibility to observation and familiar occurrence of the terrestrial Annelids, the earthworms, it is chiefly amongst this group that cases of doubleness have been observed and recorded, though such also exist amongst the marine forms.

From an examination of the bibliography of this subject as recently given by H. Friend,[1] it appears that some twenty cases are upon record, cases of double head or double tail, chiefly in the earthworms.

In the hope that the recording and description of such cases may ultimately contribute to a rational comparative teratology,

[1] 'Nature,' February, 1893.

and also prove of value in the understanding of some fundamental problems of regeneration, two additional cases of doubling of the posterior end in earthworms are here published, together with eight cases in a marine Annelid.

ALLOLOBOPHORA FŒTIDA.

The two abnormal specimens of the "Brandling" here described were taken at Bryn Mawr, Penn., in April, 1892, at the period when the conjugation process seems to be at its maximum. Some conception of the probable frequency of such duplications in this animal may be got from the facts that the first abnormal individual, which we will call A, was found amongst 480 preserved specimens collected at one time by Dr. T. H. Morgan (to whom I am indebted for much of the following), while the second individual, B, was found amongst 560 collected at different times : a third collection of 220 specimens carefully examined when alive contained no bifurcated individuals.

The first specimen, A, as seen in fig. 1, is perfectly normal down to and including the 73rd somite, where a marked bifurcation occurs. An examination of the anterior region proved that the sexual organs were normal and mature, and that the sperm receptacle contained ripe sperm, indicating that conjugation had taken place.

Posterior to the 73rd somite there are two large abnormal rings marked, like the normal somites, by dark brown bands on the dorsal surface, as seen even in this alcoholic specimen. From the second of these spring the two tails or terminals; one having 18 somites and an anal piece; the other, on the right, only 7 somites and an anal piece. There are thus $73 + 2 + 18 = 93$ somites in what seems the main axis of the animal and seven in what appears as a lateral outgrowth from the second abnormal ring. This lateral terminal springs from the right side and lies in the same plane as the main trunk, as is evident from the enlarged views, figs. 2 and 3.

In the dorsal view, fig. 2, we see that the dorsal pores are everywhere present in the normal positions, except that there are none visible at the base of the right terminal, between its

first somite and the second abnormal ring of the trunk, which we have marked 75. The dorsal pore between the two abnormal rings 74 and 75 is removed to the right, so that it lies rather in a curved series from the trunk into the right terminal than in the straight series of the trunk and main terminal. When, however, the dorsal body-wall is removed and viewed from the ventral aspect, having been made translucent by glycerine, we see, as in fig. 4, that the dorsal pores of the right terminal B are not really in the series of the trunk H; while the latter are in the same series as those of the main terminal T. The slender muscles or groups of longitudinal muscle-fibres that pass from one dorsal pore to the next are seen to bend, from the pore 74—75 over towards the animal's right to end at the pore 75—76, crossing the darkly pigmented band of 75 and half the light bands 74—75 and 75—76. The muscle that runs up from the lateral terminal becomes lost in the general dorsal muscle and is not connected with any other pore than the one 1—2 whence it starts.

The ventral view, fig. 3, together with fig. 2, shows the true shape of the abnormal rings 74 and 75. While 74 appears but slightly notched on its left side, it is subdivided ventrally by a groove coming down from the right side; it is a ring much wider on the left than on the right. So the ring 75 is, inversely, much wider on the right than upon the left; it is marked ventrally by grooves that but imperfectly separate it from the somite 1 of the right terminal. The two abnormal rings 74 and 75 together make a cylindrical mass of less diameter than the trunk or the main terminal. It is from the expanded right side of this second ring, 75, that the right terminal arises, while the main terminal is continued from its distal face.

As is seen in the ventral view, the parallel lines that mark those thin areas of the body-wall muscle along which the ventral setæ are inserted, continue from both trunk and main terminal out into the lateral terminal, or in other words, the right line of ventral setæ is continued as the right or anterior line of ventral setæ of the lateral terminal, and the left or posterior line of ventral setæ of the lateral terminal is continuous

with the right ventral line of the main terminal. This continuity of structure from trunk to terminals is seen again in the body-walls and in all longitudinally elongated organs. Thus in fig. 4 we see the muscle fibres of the longitudinal system of the dorsal body-wall passing from the trunk into both terminals.

Dissections and longitudinal sections of the terminals and their union with the trunk show that each is perfect in all the organs of a normal posterior end of an earthworm and that all the longitudinal organs of each terminal become continuous with those of the trunk. Thus, as seemed apparent from the surface (fig. 3), there is an anal opening for each terminal. The short right one has, like the larger one in each of its somites, the normal character and arrangement of body-wall, septa, digestive tract, blood-vessels, nerve cord, nephridia, and setæ. The nephridia terminate in nephrostomes and pass into the body-wall, presumably to open to the exterior, though this was not seen in the sections.

The only departures from normal structure are found in the peculiar rings 74 and 75. The digestive tract, as shown somewhat diagrammatically in fig. 5, sends out a large branch into the right terminal; the dorsal blood-vessel does the same, and so does the ventral or subintestinal vessel, as was demonstrated in serial sections. The ventral nerve-trunk bifurcates in such a way that fibres pass from each of the three diverging trunks into each of the other two. The "giant fibres" also pass from one to the other; fibres from the trunk or body pass into each terminal and fibres pass from each terminal across into the other terminal. All this takes place in a nerve mass but little smaller than and not unlike the normal, except where the actual separation of the fibres takes place.

The ventral nerve thus formed as a lateral outgrowth from, or, more accurately, as one fork of the nerve-cord of the body, has in each terminal the normal ganglionic swellings for each somite.

The septa that subdivide the body-cavity are normal in position and structure in the body and in each terminal except in

these abnormal rings 74 and 75. As far as could be made out by dissection and by section the arrangement of the septa was as indicated in the diagram, fig. 5. A large septum appears to separate 74 from 75 internally and to correspond to the external groove between those two peculiar rings. The body-cavity of 75 is bifurcated like its wall and its contents, supplying the base of each terminal, and is separated from the somites 76 and 1 of the two terminals by two distinct, complete septa. While this ring is not subdivided internally, the anterior one, 74, presents on the left four small, incomplete septa extending from the body-wall to the digestive tract, as seen in fig. 5. Each compartment of the body-cavity so formed has its own cluster of small setæ, five pairs in place of one on this left side. On the right side no setæ could be found

The nephridia that are normally present in both terminals, as indicated in fig. 5, seem to be absent in 75 on its right, where we would expect one either posterior to or anterior to the branch of the intestine that runs out into the right terminal; it may have been displaced and not recognised in the serial sections. The nephridia of 74 are multiplied on the left to correspond to the number of subdivisions of the body-cavity, five nephridia taking the place of one.

One other abnormality shown in the diagram should be mentioned, as it makes the exception to the rule that all the abnormalities are within the two rings 74 and 75; the ring 1 of the right terminal has no nephridium upon the left side, as far as could be ascertained.

The ring 75 thus bears both the terminals and contains all the bifurcated organs; it appears to be a single somite.

The ring 74 is single upon the right but subdivided upon the left. From the small size and apparent newness of these small septa and setæ we may judge them to have been interpolated here to make what were else a normal ring so much longer upon the left than upon the right. If this elongation of the left side of 74 were non-existent the two terminals would appear, obviously, as two sister structures or as a bifurcation of the main axis, not as a main terminal and a side outgrowth.

The abnormality of this specimen, A, thus expresses itself not only in the duplication of the posterior somites but in an elongation of the trunk upon one side with partial formation of somites there.

The second specimen, B, is much less conspicuously bifid, having only a small bud-like outgrowth upon its left side near the posterior end, as shown in fig. 6. There is here no doubt that the right terminal is the normal continuation of the body while the left terminal is of much subordinate importance.

This individual was sexually mature like the other; dissection of the anterior region showed that the reproductive organs were perfect and mature and that the dorsal receptacle contained sperm; there were also two "spermatophores" attached to the exterior upon the ventral side.[1]

A very important peculiarity of this specimen is seen in fig. 6, that is that all the somites posterior to the 59th are short and crowded with numerous double or abnormal rings, and that all this posterior region is noticeably narrower than the anterior, so that we at once infer, from the specimen, that all the region posterior to the 59th somite is a new formation due to regeneration of the original terminal. This seems to be a pretty safe conclusion, though there is still the chance that the narrowness of this region may have been due to incomplete development, to some deficiency in the early embryo or larva.

The entire number of somites as counted on the right side, where several split or double rings increase the number, is 103, and an anal piece so bent ventrally as to be invisible in the dorsal view, fig. 6. Of these about nine are posterior to the bifurcation, counting the anal piece as one; in the left lateral process there are also nine divisions, including the final or anal piece, which, however, shows no sign of an anal opening.

The dorsal and ventral views, figs. 7 and 8, show that there are considerable irregularities in the somites anterior to as

[1] I hope to show elsewhere that in A. fœtida the dorsally placed sperm-receptacles are filled during conjugation, and that the so-called "spermatophores" are almost accidental structures, which fall off soon after the act of conjugation.

well as posterior to this left lateral outgrowth, while this itself seems normal in the character of its rings. Thus the somite 90 is a single ring while 89 is split on the left side, or forms as it were a ring the ends of which somewhat overlap one another. 91 and 92 as counted on the right are continuous by a spiral of one turn. Thus, as may be easily seen in a model constructed from the above figures, the anterior part of 91 is a complete ring that is continued from its middle dorsal part as a spiral passing to the left, down, and across the ventral side, to come up again into the dorsal side on the right; here it forms the anterior part of 92 and is continuous with the complete ring that the posterior part of 92 forms.

The dorsal pore seems to be lacking at the beginning of this spiral, where 91*b* leaves 91*a*, but it is present at the other end where 92*a* joins 92*b*. The spiral may be designated 91*b* + 92*a*.

The next rings, 93 and 94, are complete and single.

The lateral process springs from the left of a complex spiral beginning in 95. Here again a clay model or a glass tube or bottle with the intermetameric groove marked upon it will make clear the actual state of things represented in figs. 7 and 8. The anterior part of 95, 95*a*, is a complete ring whence a spiral, 95*b*, runs over toward the right and so around across the ventral side, in a direction opposite to that of the spiral 91—92. This spiral 95*b* comes up on the left as 96 and so across and down to end on the ventral side in a complete ring, 97, fig. 8. This spiral thus makes one and a half complete turns from the ring 95*a* to the ring 97.

Certain complications must next be considered. The ring 95*a* is subdivided ventrally by a faint groove, seen only in fig. 8, into two half rings $95a^1$ and $95a^2$ corresponding to the single ring 95*a* as seen on the dorsal side. Again, the region on the left whence springs the lateral terminal is an elongated elliptical expansion of the union of 95*a* and 95*b*, as seen from the left side. This enlarged lateral region ends ventrally, fig. 8, in a sharp angle between the divaricated 95*a* and 95*b*; the enlarged region crowds the halves of 95*a* ($95a^1$ and $95a^2$) in front of it and crowds behind it the ring 95 *b*, where continued

as 96, on the left side of the animal. The dividing line between 95 *a* and 95 *b*, bifurcates to send one limb anterior to the enlarged region, the other posterior to it; the former limb stops abruptly at the union of lateral and dorsal surfaces, and so appears as a mere notch in the left edge of 95 *a* as seen in fig. 7; the posterior limb continues as the line between 95 *b* and 96, fig. 7. An additional complication appears in fig. 8, where a small furrow, X, is seen posterior to the lateral outgrowth; it extends only a short distance upon the ventral and lateral faces of the enlarged region.

The lateral process may thus be regarded as springing from the enlarged left side of the spiral as it starts from 95 to run over to the right, the enlarged area dropping down to the left enough to be visible upon the ventral surface.

The existence of this spiral makes less obvious the similarity of this case to the first, A; but for the spiral the lateral process would arise from the left side of 95 *b* much as does the process from the right side of the ring 75 in the specimen A.

Posterior to the ending of the spiral in the ring 97 there are six normal rings and a normal anal piece and anal opening (fig. 8).

Turning near to the left terminal we observe that it has eight rings, the first somewhat subdivided by a short groove, and an anal piece that is not perforated by any anal opening. The colour bands and retæ are evident externally. The absence of anal opening is found upon examination to be accompanied by the entire absence of any digestive tract.

The entodermal parts of this lateral outgrowth of eight somites were entirely wanting.

In a cross-section of the middle part of the process we find the body-wall made up of the normal epidermis, longitudinal and circular muscles and peritoneal lining of the body-cavity. The histology of these is, however, much as in a young immature animal or as in a regenerated posterior part. There are dorsal and ventral setæ, a ventral nerve-cord, and large nephridia of the type found in this species. The saccular terminal parts of these nephridia are, however, very much distended, so that the pair of nephridial sacs take up most of the space usually

occupied by a digestive tract. There is no dorsal blood-vessel, but the subintestinal blood-vessel is represented by a trunk that pierces all the septa and is traceable to the sub-intestinal blood-vessels of the trunk, of which vessel it is a side branch.

The only organ that seems to indicate a digestive tract is a peculiar strand of muscles forming a slender cord running the whole length of the body-cavity dorsal to the nerve-cord. This muscle pierces the septa, and closely accompanies the above-mentioned ventral blood-vessel, lying just dorsal to it. It may, perhaps, be regarded as a representative of the musculature of the digestive tract.

The body-cavity contains numerous amœboid corpuscles. The ventral nerve-cord presents a ganglionic enlargement in each somite, and is accompanied by subneural and by lateral blood-vessels. Its sheath is but little developed, and its histology presents indications of immaturity, though showing the normal ganglion cells, giant fibres, and fibrillar substance.

In such a section the only departures from the normal are in the absence of digestive tract and dorsal vessel, in the incomplete histological state, and in the presence of a free supra-neural muscle-cord.

A transverse section near the posterior tip, fig. 9, shows most of the structures as seen at the middle of the process, but the tissues are still less perfected and the ventral blood-vessel and its accompanying supra-neural muscle are absent. There is in addition at this part of the process a peculiar septum dorsal to the nerve-cord, which here is just separating from the body-wall. This partition is only the last septum much inclined along with the ventral bending of the tip of the process, so that it cuts off a small terminal part of the body-cavity on the ventral side around the nerve-cord from a larger, really more anterior, part that lies dorsally and contains the large nephridia. As the nerve-cord sinks down completely into the body-wall near the extreme tip of the process, there is left above it a small pocket of the body cavity, shut off from the rest by the above oblique partition yet open anteriorly

into the cavity of the penultimate region 8. Owing to the absence of the digestive tract, the appearance of the tip of the process is quite peculiar in section, and this backward extension of the penultimate body-cavity space makes it the actual termination of all the sections. Thus the last appearance of the body cavity is as two small pits in the body-wall, on either side of a ridge that passes along where the nerve-cord is about to emerge from the ventral body-wall; these are ventral and belong to the region 8. Dorsally, the terminal region 9 ends bluntly, with no trace of any anal invagination or indications of a digestive tract.

In other words, the septum between 8 and 9 sends back a nearly horizontal arch over the nerve-cord, and then cuts off a small ventral cœlomic space that ends at the extreme tip of the process as a pair of pits, one right and one left of a slight median ridge.

Where this peculiar left process joins the main trunk of the animal we find all its longitudinal organs continuous with those of the trunk; the nerve-cord joins the main nerve-cord, the ventral blood-vessel the main sub-intestinal vessel, and the longitudinal and circular muscles are directly continuous with those of the main trunks.

The digestive tract of the trunk is in no way affected by the presence of the lateral process.

As might be anticipated from the external views (figs. 7 and 8) the arrangement of the septa in this region of union is by no means simple nor readily made clear. As will be seen in the horizontal section (fig. 10), the septa here are much enlarged and distorted, so that they lie beyond the planes of demarcation between external rings.

With some considerable success we may attempt to trace a septum for each external groove, but errors easily creep in.

In the lateral process itself the septa are but elongated and forced inwards towards the trunk, so that from 3—2 and 2—1 we pass to the much distorted septum 1—95 that reaches in almost to the digestive tract of the trunk. Each body-cavity has its appropriate nephridia.

In the trunk many irregularities occur. A remarkable long septum runs nearly parallel to the digestive tract anteriorly separating 94 from 95 *a*, and posteriorly 95 *a* from 95 *b*. It is connected with the walls of the digestive tract by two short septa that may be regarded as the continuations of septa 94—95 *a* and 95 *a*—95 *b*, though this continuity was not demonstrated.

An examination of the series of sections shows that this longitudinal septum is not continuous, but of slight extent. It may be regarded as a veil stretched between 94—95 *a* and 95 *a*—95 *b*, which seem to be complete transverse septa. Some additional complexities affect this region.

As indicated in this figure, nephridia are found in most of the chambers of the body-cavity, right and left. In 93, on the right, there is one of the peculiar masses of old setæ and leucocytes so often found near the posterior end of earthworms. In addition, this part of the body-cavity contained a normal nephridium. As far as could be ascertained the nephridia are absent in the left of 94 and 96, but they may have been destroyed in a dissection previous to sectioning.

PODARKE OBSCURA.

This small polychætous Annelid is exceedingly abundant in the "eel-pond" at Wood's Holl, Mass., where it may be seen crawling upon the eel-grass or upon the muddy bottom, or occasionally swimming free.

My attention was called to the occurrence of bifid monsters in this species by Mr. A. L. Treadwell, of Miami University, Oxford, Ohio, who observed as many as fifteen cases of bifurcations of the posterior end, none of the anterior end, amongst 1500 or more individuals examined in the summers of 1891 and 1892. Although less than 1 per cent. were abnormal, yet a collection of about 100 taken at one time showed five or six bifid monsters.

Regarding these he writes :—"The tail sometimes branches equally, so that there is no difference between the sides, and sometimes the second portion is much smaller than the other.

It may in some cases branch out one third of the way towards the head from the tail, and is then usually at right angles to the body proper. This branch may be so small as to be a mere bud, or it may attain a considerable length. I think that both sides are supplied with intestine and nerve-cord."

To his courtesy I am indebted for three of these specimens, as well as for five others obtained the past summer, 1893, at the same place.

For convenience these eight cases of bifurcation of the body posterior to the head region may be referred to as the specimens A, B, C, V, W, X, Y, Z.

The first, A, was in alcohol, having been carefully hardened for examination by means of sections. The other two, B and C, were stained and mounted in Canada balsam.

The general flat, broad shape and colour of this Annelid are indicated in fig. 16, which, however, is not as dark as the animal usually appears.

In the specimen A the body is bifurcated in such a manner that there are two equal terminals, one dorsal and one ventral, as seen in the side view (fig. 11). At the same time each terminal may be regarded as a right or a left branch, since their tips diverge widely from side to side as well as up and down, and since, moreover, the terminals and trunk come together obliquely, that is, the dorsal terminal is somewhat twisted towards the right, the ventral one slightly towards the left, or as we may express it, the median planes of the three parts diverge and are twisted so that they have no line in common, only a point.

The parapodia continue along the ventral or right terminal with little interruption in their line of sequence, but the parapodia of the dorsal terminal are separated from those of the trunk by a wide interval, and do not have the same direction as those of the trunk. In fact, the dorsal terminal looks like a dorsal interpolation grafted upon the trunk where it bends down, and somewhat to the right, as the ventral terminal.

In this specimen the number of setigerous somites in the trunk or region anterior to the bifurcation is 27, while in each

terminal there are just 8, so that there are 27 + 8 = 35 setigerous somites in the main line, with a duplication of the posterior 8 arising between the 27th and 28th somites.

Before speaking of the internal anatomy of this individual we may note that the other two, B and C, have almost the same character, the same oblique insertion of the terminals, but different numerical proportions. The specimen B has 23 somites in the trunk, 12 in the right and 11 in the left terminal. The specimen C has only 18 somites in the trunk, 10 in the left and 8 in the right terminal, which latter is broken.

In all cases the terminals are all complete, as far as can be judged from an external examination of the general form, in proportions, parapodia, anal termination, and ventral nerve trunk.

On studying the internal structure of A, by means of serial sections, we find at once that the two terminals almost exactly repeat the normal anatomy of the trunk, and are thus like two normal posterior ends of two normal Annelids. Each terminal has the normal digestive tract, nerve-cord, blood-vessels, and muscles, as well as setæ and parapodia and even reproductive organs—the mother-cells of sperms.

At the point of divarication the body-cavity and the digestive tract branch, as shown in fig. 12, which represents a median ventral section of the specimen A.

Each terminal has its anal opening and its ventral nerve-cord extending forward from the anus throughout all its somites; but while the nerve-end of the ventral terminal is continued on as the ventral cord of the trunk, the nerve-cord of the dorsal terminal stops suddenly in the first somite, as shown in the figure. It thus appeared that the dorsal terminal was imperfect in having its nerve-cord imperfect in the first somite and without connection with the nerve-cord of the main trunk of the animal. A careful examination of the entire series of sections shows that this is probably the case. The nerve-trunk in the first somite is free from the epidermis, in which it normally remains in Podarke, and gives off large nerves along certain muscles which radiate upward from the nerve-

cord to the intestine in each somite. Here, in the intestine, the nerves were lost, and could not be followed into any connection with the main trunk of the animal. The nerve-cord ends bluntly as an upturned mass, suggesting a former connection with, and rupture from, the main ventral nerve-cord of the animal.

The lateral nerves that run out in the epidermis to the parapodia are found in the first somite as in the others, but there is no indication of any lateral nerve establishing a connection between the ventral nerve-cord of this dorsal terminal and the nerve-cord in the main trunk.

To determine if this peculiar behaviour of the nerve-cord was found in the other two specimens, B and C, they were prepared and cut into serial sections, crosswise. It was then easy to see that the same conditions obtained here as in specimen A. In both B and C the body-cavity bifurcates, and the digestive tract bifurcates and runs out into each terminal as if to an anal opening (which, however, was not demonstrated). Yet the nerve-cord does not bifurcate, but passes directly into only one of the terminals, the left one in each case.

The other terminal, the right, has its normally formed nerve-trunk that stops near the base, with no indication of any direct connection with the main system.

In other respects the two terminals in B and C are normal and alike. The dorsal and ventral blood-vessels and the muscles are all perfectly normal; and the body-cavity, as in the more anterior region of the body, contains large masses of young reproductive cells, sperm mother-cells, in each terminal.

In these three specimens we find the terminals normal repetitions of the posterior end of the body, except that the more dorsal terminal, the one more to the left in A, but the one more to the right in B and C, has no apparent connection with the nervous system of the anterior part of the body, and is thus isolated in a peculiar manner. This isolation was entirely unexpected, since in all other cases of bifid Annelids the nerve-cord, as far as there are any statements made about it, is said to bifurcate also and to send a branch into each terminal.

The five other specimens taken by Mr. Treadwell in the summer of 1893 may now be described in detail.

The individual V, taken August 18th, was not normally active, but rather torpid; it lived but three days in captivity. The bifurcation, though visible to the naked eye when once noticed, was not conspicuous, but, on the contrary, easily overlooked.

The supernumerary terminal has the form of a small bud from the right side, as seen in fig. 13, which appears to the naked eye as a new parapodial-like mass interpolated between parapodia 33 and 34 on the right side, but is in reality a complete posterior end with five normal somites and normal anal tip and cirri.

This small lateral terminal is so far imperfect in that the basal or first somite has an imperfect parapodium upon its left or posterior side, as seen in the figure. This parapodium is small and not complete ventrally, so that a ventral view would show only four parapodia upon the left side of the small terminal and five upon the right. This lateral process or terminal stands out nearly at right angles to the main trunk, but points somewhat downward or ventrally. Its ventral surface is continuous with that of the trunk, but its dorsal surface does not extend up to the level of the dorsal surface of the trunk, but ends between the parapodia as indicated in the figure.

Judging from the size and appearance of the last or 5th somite, the lateral terminal is young and actively growing. It is well pigmented, and otherwise like a normal terminal in appearance. The somites 2, 3, 4, show the same dark masses upon each side of the intestinal tract that normally occur upon the intestine in the rectal region in Podarke.

Posterior to this minute terminal there are 13 somites in the main line of the trunk, which makes a total of 46, in addition to the five small ones of the lateral outgrowth. The body ends abruptly in an anal piece that has evidently recently replaced one lost by accident; as yet no anal cirri have developed, but the long dorsal cirri of the last somite are directed backward, as is common when the anal end is lost.

Serial sections show that the minute lateral terminal has the normal internal structure: the main digestive tract and the ventral nerve-cord send each a branch into the terminal and so through the length of it. This side intestine ends in an anal opening at the tip of the terminal.

The animal is evidently an immature female with developing ova in the ovaries of the trunk and very young ovaries in the basal somites of the terminal also.

This individual is also remarkable for the abnormal development of many of the parapodia upon the main trunk. As represented in fig. 14, the tip, in many of the parapodia, is not a single cone but bears from its posterior face a conspicuous outgrowth, $\times$, which causes the parapodium to appear forked or bifid from a dorsal view.

The specimen W, taken August 17th, has a large, swollen dorsal and a small ventral terminal as seen in the side view, fig. 15.

In life the swollen dorsal terminal is lighter in colour than the dark trunk and appears as if filled by a milky mass as of sperm. It is wider than the trunk at this region and has nine somites that are short, as if contracted. The tail end is truncated, the anal piece together with some few somites having been lost. It stands up abruptly from the posterior edge of the 25th setigerous somite.

The small ventral terminal has but little colour, an appearance of being a new growth and an anal end that seems to be growing. It is made up of six setigerous somites and a seventh with slight parapodial outgrowths as well as an anal piece with one anal cirrus present.

It stands nearly horizontal but yet pointing decidedly downward, at times making an angle of nearly 45°. Having but little pigment in its dorsal surface, the blood in the dorsal vessel may be seen passing forward towards the trunk.

The animal crawls and swims with the dorsal terminal raised stiffly. When stimulated by touches from a needle, the dorsal terminal seems less sensitive than the ventral one, partly, perhaps, because it has no anal cirri. While a gentle touch to

the ventral terminal will often produce active crawling or even swimming, such a touch often causes the dorsal terminal merely to shrink without setting up any locomotion in the entire animal.

Sections show that there is a complete bifurcation of the digestive tract, so that the small ventral terminal has an anal opening that communicates with the main intestine, while the dorsal terminal is also provided with a branch of the intestine proceeding towards the wanting anal piece.

The large dorsal terminal contains much sperm or masses of nearly ripe sperms, and the trunk as well as the small terminal contains male cells. The nerve-cord continues from the main trunk directly down into the ventral terminal, and so out to its anal tip. A normally developed nerve-cord is present in the dorsal terminal, but there it ends abruptly without any traceable connection with the nerve-cord of the trunk.

We meet here again the same peculiar condition found in A, B, and C, and have an explanation for the differences observed in stimulating one or the other of the terminals: the dorsal one has an interruption in its nervous connection with the anterior part of the body, and hence when stimulated does not readily set up movement in that part of the body.

Sections of this region show the same anatomical relations as are indicated in fig. 12.

The individual X was a large ripe female, found among several hundred adults taken at different times in July. Being full of ripe eggs the body readily ruptured, and was not studied alive.

An examination by section showed that the eggs and ovaries fill not only the main trunk, but also both terminals.

Of the two terminals the smaller one arises as a lateral outgrowth from the right, much as in fig. 13. It is, however, much larger than in that specimen, though shorter and narrower than the main terminal.

It springs from the right side between the parapodia of the 29th and 30th somites, which it forces widely apart. At first turned outward, it then bends backward, so as to lie more nearly parallel with and dorsal to the main terminal. It is

inserted obliquely, so that its median plane is not vertical, but inclined so that the right side is turned downward and the left side upward. It is so attached as to occupy all the space between parapodia 29 and 30, and then extends upward somewhat upon the dorsal aspect of the trunk, so that its left or more posterior face is continued out from the dorsal surface of the somite 30 where it joins 29. Ventrally the attachment extends no further than the ventral part of the parapodia. The parapodia upon the left of the bud, near its base, overhang the back of the main terminal.

The length of the lateral terminal is 2½ mm., that of the entire main axis 12 mm., of which 9 mm. is anterior to the point of bifurcation and 3 mm. posterior to it.

The main axis has 42 somites, of which the last three are quite small and young; 29 are anterior to the bifurcation, and 13 posterior to it. The lateral terminal also has 13 normal somites, and an anal piece on which the anal cirri are lacking, from accident apparently.

Owing to the rupture of the body in dying, no idea of the internal anatomy of the point of divarication of the terminals was obtained. Both terminals have the normal internal organs, even ovaries, as above stated.

The specimen Y was taken amongst two or three hundred, August 3rd. It has the general appearance of W, as shown in Fig. 15.

Of medium size, it swam about actively or crawled upon the bottom of the aquarium.

The main trunk has 27 setigerous segments, the ventral terminal 6, and the dorsal 7, but it is truncated by the loss of its normal tip and several somites.

The dorsal terminal is much stouter and longer than the ventral one. The latter does not extend across the entire width of the trunk, but arises as a sort of outgrowth from the left half of the ventral face.

The somites 25, 26, 27, are contracted and narrow from side to side; 25 and 26, judging from the appearance of the parapodia, have been injured upon the right side.

When the animal was alive the dorsal terminal stood nearly vertical and the ventral nearly horizontal while swimming, but in crawling the ends were inclined at about 45° to the horizon and so at right angles to each other. After death the dorsal terminal projects horizontally nearly in the line of the main trunk, while the ventral one now stands nearly at right angles to the rest. The ventral terminal is of some use in crawling, since its parapodia perform regular, rhythmic crawling movements. The dorsal terminal is of no use in crawling, as it is raised above the surface, yet its parapodia at times move, but in an irregular manner. The dorsal terminal may move back and forth to vary its angle with the trunk, and at times it makes undulating movements from side to side, as does the trunk, in swimming.

The colour of the animal is normal; the dorsal side of each terminal is marked by the normal transverse bands of dark. As the animal swims, the anterior face of the dorsal terminal and the posterior face of the ventral terminal, being the dorsal aspects, are dark brown, while the posterior face of the first and the anterior face of the second, being the ventral aspect, are light coloured.

As the colour bands of the dorsal terminal are somewhat lighter than those of the ventral, it has a new or grey appearance which does not harmonise with the anatomical conditions found upon sectioning.

When stimulated by the touch of a needle to the head, antennæ, or cirri, the anterior region shrinks back. When the end of the ventral terminal is so stimulated there results a forward movement of the whole body, there may be even a rapid swimming away. Stimuli applied to the dorsal terminal cause local movement, but no change in the anterior region unless the stimulus is strong, when the animal may crawl, but not swim. It thus appears that the dorsal terminal is not as perfect a medium for transmitting stimuli to the entire animal as is the ventral.

Examination of the internal anatomy shows the same condition of affairs found in A, as seen in fig. 12. While the

digestive tract bifurcates to furnish an arm to each terminal with an anus at the tip of the ventral and, presumably, one at the tip of the dorsal when the tip was present, the nerve-cord does not bifurcate.

The nerve-cord of the trunk runs down to the anus as what seems to be, judging from its histological appearance, a new nerve-cord along the median ventral line of the ventral terminal. The nerve-cord of the dorsal terminal ends abruptly where the ventral surface is continuous with the dorsal surface of the other terminal. It has no connection, so far as discovered, with the main nerve-cord.

The sections also show that Y was a female with ovaries both in the trunk and in each terminal; the ovaries are as yet only small masses of cells with large nuclei.

The last specimen, Z, was found amidst several hundred, August 6th. It differs from all the others in having the bifurcation far forward as a small lateral terminal upon the left, as seen in fig. 16.

At rest upon the bottom of the aquarium the animal is straight or variously bent, generally so that the lateral process projects at acute or obtuse angles or at right angles with the straight or convex side of the body, rarely is the animal bent so that the process projects from a concave line. The curvature of the body may be uniform anterior to and posterior to the lateral process, or there may be a separate curvature on each side the region of the process; posterior to the process double curves, right and left, were observed.

In swimming, the body is nearly straight and the process projects nearly at right angles.

From the general coloration of the body, as indicated in fig. 16, the process makes an exception as regards the left or anterior side of its dorsal face. On this half the transverse colour bands are very imperfect, existing only upon the side between the parapodia and not extending up on to the dorsal surface. The posterior or right half has, however, the normal arrangement of bands. Along the lighter coloured left side there extends a clear streak, like a scar, reaching from near the

third left parapodium back nearly to the anal end in a somewhat oblique course.

The dorsal blood-vessel is plainly seen in this process and left terminal as well as in the main trunk and in the main terminal. The vessels contract in each terminal with about the same rhythm, so that blood flows simultaneously from each forward into the anterior region of the body.

In other respects the lateral process has the normal appearance of a normal terminal, excepting that the anal piece and the anal cirri are smaller than in the main terminal, appearing to be young.

The ventral surface shows a ventral blood-vessel that bifurcates to enter each terminal, and there is also an indication, in the live specimen, that the ventral nerve-cord also bifurcates.

When the lateral terminal was touched it contracted, and sometimes there was also a movement of the anterior region, but rarely was there any movement of the posterior region or locomotion of the entire animal. If the anal region of the main terminal was touched a locomotion of the entire animal was pretty sure to follow.

When not stimulated the animal exhibited but little motion.

As seen in fig. 16, the number of setigerous somites is 16 anterior to the bifurcation, 14 in the lateral terminal and 25 posterior to it, making a total of 45, of which 31 are in the main axis and 13 in the lateral duplication.

The entire length, in life, was $10\frac{1}{2}$ mm.; the length of the process 2 mm. This process springs from the 17th setigerous somite at a point 4 mm. posterior to the head end and $6\frac{1}{2}$ mm. from the anal end.

An examination of the internal anatomy shows that the process has the normal organs; its digestive tract is a branch of that in the main trunk; the nerve-end is a branch of the main cord; the body-cavity is filled with a number of sperm mother-cells. There is a complete bifurcation or branching of all longitudinal organs in such fashion that each terminal gets one branch; those to the smaller terminal appear as side

branches from the main system found in the trunk and directly continued into the main terminal. The side terminal repeats all the organs of the main terminal, having digestive tract, nerve, blood-vessels, muscles, reproductive cells (male), and anal opening, just as in the main terminal. It is an exact repetition, and differs only in small size, fewer somites, and abnormal coloration upon its left dorsal half.

The following table will serve as a summary of the general character of the above eight abnormal specimens of Podarke.

The first column gives the number of somites anterior to the bifurcation, the second the number in the right terminal, the third those in the left, the fourth the entire number in the chief or main axis, while the entire number of all the somites is given in the last column.

A,	♂	27	8	8	35	43
B,	♂	23	12	11	35	46
C,	♂	18	8+	10	26+	36+
V,	♀	33	5	13	46	51
W,	♂	25	9+	6	34+	40+
X,	♀	29	13	13	42	55
Y,	♀	27	7+	6	34+	40+
Z,	♂	16	25	14	41	55

Conclusion.

From the above description we find that these ten cases of bifid monsters agree with those previously described amongst the Annelids in that we have to deal with a complete duplication of part of the body, the main axis and all its appurtenances being exactly duplicated for a certain distance. The only exception, and a very marked one, is the earthworm B, which has a side duplication in which the entodermal part is absent. This absence of entoderm in what is otherwise a normally developed and metameric region of the Annelid, is of considerable interest with reference to the cœlom theory and its applications to the explanation of metamerism. When so perfect a metameric part of an Annelid may be formed, even abnormally, without the presence of an entodermal core, we have an additional reason for doubting that the ultimate explanation of

metamerism can be found in the idea that "gut-pouches" are the first steps.

The questions as to the time of formation and the causation of such monsters remain still open. Whether they arise in the adult or in the embryo is as yet undetermined. Yet the balance of evidence seems to point to the conclusion that such bifurcations may be produced in the adult.

While such a very unusual, in fact unique, specimen as the earthworm B might have arisen from such an abnormal larval form as figured and described by Mr. Wm. E. Ritter[1] for Polygordius, we might just as well imagine it formed as the result of abnormal regeneration after traumatic interference. All the other cases may be easily explained upon the assumption that removal of the normal terminal, or injury to it, has resulted in regeneration of such abnormal sort that more than the last part has been re-formed, either two complete terminals to replace one, or else one complete terminal instead of the injured part of the normal one.

Some cases lend themselves to this explanation more easily than to any other; in fact, some cannot be explained upon any other assumption than that the duplication has arisen in the adult. Such a case is that of the doubled-headed Annelid observed by Langerhans, which, as previously noticed,[2] could scarce have attained such dimensions without the former presence of a larger head that was then replaced by two small ones in abnormal regeneration.

Again, in the earthworm B there are indications that the entire region posterior to the 59th somite has been regenerated, which would mean that the bifurcation was formed in a late stage. Then, in the eight cases studied in Podarke, anatomical and physiological facts point to the conclusion that in five of them, namely A, B, C, W, Y, one of the terminals has no, or no direct, nervous connection with the head-end; while its well developed and large nerve-cord ends abruptly, as seen in fig. 12, in such a way as to force upon us the idea that there was

[1] 'American Naturalist,' December, 1892, pp. 1047—50.

[2] 'Ibid., September, 1892, p. 730.

formerly a connection of this nerve-stump with the main nerve-cord, an idea that is strengthened by the often immature, young appearance of the other terminal. We naturally suppose here that a wound has healed over in such a fashion that the old nerve-cord does not reunite, but that the distal end remains as an isolated stump while the proximal end grows down into the new terminal that is formed, abnormally, in place of the injured tissue, or at the place of injury to the tissue of the normal terminal.

As there thus seemed some probability that operative interference would result in the regeneration of the terminals in some cases, many experiments were performed on earthworms and upon Podarke. The results were negative. After the most various injuries,—removal of the posterior end, lateral, dorsal, ventral injuries, hemisection, cutting or cauterising,—there resulted a normal healing of the wound or else the regeneration of a normal terminal, never a duplication. This, however, is not astonishing, considering the rare occurrence of such duplication even in nature, where, no doubt, similar experiments are constantly being made. In fact, if the hypothesis be true that such bifurcations arise in process of regeneration, we would not expect it to occur often, as in nature both Allolobophora fœtida and Podarke obscura very frequently lose and regenerate the posterior end, but very rarely produce a bifid termination. Thus, though such negative experiments tend rather to impress one with the remarkable tenacity with which the organism adheres to its normal form, and suggest to one's mind the presence of some controlling law like that denominating the formation and regeneration of a crystal, they furnish no evidence against our assumption.

Granting provisionally that bifurcation in Annelids in all cases may be, and in some cases must be, due to abnormal processes of regeneration, we may advance the working hypothesis that these processes consist in the interference with the normal position or conditions of the cells concerned in regeneration. That is, we need not invoke the activity of any unusual amount or character of idioplasm, no special manipu-

lation of "supplementary determinants" seems necessary if we seek to apply here the facts worked out for the cleaving ovum by Driesch and by Wilson. As there the partial separation of cells or their affectation by various external agents may determine their action in groups to produce more or less separate individuals in place of one single individual, so here we may suppose that injuries and other external agents affect the regenerative tissue so that the same cells that else had formed one normal terminal now form two more or less separate ones.

JOHNS HOPKINS UNIVERSITY,
BALTIMORE; December 7th, 1893.

EXPLANATION OF PLATES 32—34,

Illustrating Mr. E. A. Andrews' paper, "Some Abnormal Annelids."

All the figures are drawn with a camera lucida excepting Fig. 1.

Figs. 1—10 are of Allolobophora fœtida. Figs. 11—16 are of Podarke obscura.

FIG. 1.—Dorsal view of specimen A taken soon after death in weak alcohol.

FIG. 2.—Dorsal view of the posterior end of A, much magnified.

FIG. 3.—Ventral view of the same region.

FIG. 4.—View of the longitudinal muscles of the body-wall at the region of union of the bud B, the tail T, and the anterior region H of this same specimen; seen from the ventral aspect. Three dorsal pores are shown in the non-pigmented intersegmental regions.

FIG. 5.—Somewhat diagrammatic longitudinal view obtained from sections of the region of union of the two terminals and the trunk, specimen A.

FIG. 6.—Dorsal view of specimen B.

FIG. 7.—Dorsal view of the posterior part of specimen B, much enlarged.

Fig. 8.—Ventral view of the posterior part of specimen B, much enlarged.

Fig. 9.—Transverse section of the left terminal, or lateral process of specimen B near its posterior tip, showing absence of digestive tract, the character of the body-wall, nerve-cord, ventral setæ, and nephridia.

Fig. 10.—Longitudinal horizontal section of the region of union of the two terminals and the trunk of specimen B, showing arrangement of body-wall, body-cavity, digestive tract, septa, and nephridia.

Fig. 11.—Right side of the posterior end of Podarke A, from an alcoholic specimen. The dorsal terminal should appear as if somewhat rotated towards the right.

Fig. 12.—Vertical median section of Fig. 11, showing the bifurcation of the digestive tract and the interrupted nerve-cord of the dorsal terminal, as well as the connected nerve-cord of the ventral terminal.

Fig. 13.—View of part of the right side of Podarke V to show the small right terminal from its dorsal aspect.

Fig. 14.—Dorsal view of one of the abnormal parapodia of the main trunk of V, showing the posterior process ×.

Fig. 15.—Side view of Podarke W from an alcoholic specimen with proboscis partly extended.

Fig. 16.—Dorsal view, much enlarged, taken from the specimen Z in life.

Studies on the Nervous System of Crustacea.

By

Edgar J. Allen, B.Sc.Lond.

With Plates 35 and 36.

I.—Some Nerve-elements of the Embryonic Lobster.

The observations to be recorded in the following paper were made at the Laboratory of the Marine Biological Association in Plymouth, with the assistance of a grant made me by the Government Grant Committee of the Royal Society. My thanks are due to the officials of the laboratory for their constant support, to the committee of the British Association, Robert Bayly, Esq., of Plymouth, and Professor E. B. Poulton, for supplying me with nominations to the laboratory, and to Professor Weldon for advice and help.

The remarkable results obtained by recent investigators of the nervous system of Vertebrates, by making use of embryos and very young animals, led me to try a similar plan in an attempt to obtain an insight into the structure of the Crustacean nervous system. The two methods used have been Ehrlich's methylene blue method, as modified by Biedermann[1] and Apáthy,[2] and the rapid method of Golgi, as modified by Ramon y Cajal, Kölliker, and Nansen. Of these, up to the present,

[1] Biedermann, "Über den Ursprung und die Endigungsweise der Nerven in den Ganglien wirbelloser Thiere," 'Jena. Zeitschr.,' Bd. xxv, 1891.

[2] Apáthy, "Erfahrung in der Behandlung des Nervensystems für histologische Zwecke. I. Methylen blau," 'Zeitschr. wiss. mikr.,' Bd. ix, 1892.

the methylene blue has yielded by far the most satisfactory results, and the observations recorded in the present communication have been made by its means.

After experiments upon a number of embryos and larvæ of smaller Decapods (Palæmon, Palæmonetes, Crangon, Virbius), which failed largely on account of the rapidity with which the fine fibres assumed the beaded form, and subsequently broke up under the influence of the reagent, an excellent object was found in embryos of the lobster (Homarus vulgaris). The fibres are here much coarser, and appear to be able to retain their normal shape for a longer time. Another great advantage of lobster embryos is their size and the comparative ease with which the thoracic ganglia can be exposed. All that is necessary for this purpose is, with a pair of needles, to burst the yolk and remove it, together with the investing membranes of the egg. It is well also to remove the connective-tissue bands (endosternite) which lie across the thoracic ganglia, especially over the portion immediately behind the œsophagus. With a little practice this may be readily done in healthy embryos without injury to the underlying ganglia. These operations may be performed in sea water, or in dilute methylene blue solution.

With regard to the strength of the methylene blue, it has been my practice to keep a standard solution of $\frac{1}{10}$ per cent. in normal salt solution, and this has been diluted with fifteen or twenty volumes of a mixture of three parts of sea water to one of fresh immediately before use. The staining is most satisfactory when the temperature is from 20° to 25° C.

The embryos, after being prepared as described, are placed on a slide, with the thoracic ganglia uppermost, and covered with methylene blue solution. The process of staining may then be watched under the microscope from its commencement. For this purpose no cover-glass should be used, and the object should be illuminated with an Abbé condenser, the diaphragm of which is left open.

The stain enters the ganglia in two ways: (1) through the lateral nerves, and (2) through any wounds which may exist in

the ganglia themselves. By taking advantage of the latter fact, many of the results to be recorded have been obtained. The ganglionic cord has been injured or cut across in various places, and some elements can be got to stain with considerable certainty by wounding in particular places. No very definite directions, however, can be formulated on this point, but a little practice will give the desired result. Accidental surface wounds, made when preparing the embryo, are often of great value in this way.

The preparations may be fixed in a solution of ammonium picrate containing an excess of ammonium carbonate, and mounted in glycerine diluted with an equal volume of the fixing solution. A large number of preparations were fixed in this way. They do not appear to be quite permanent, but preparations which I have kept for five months, although they have lost some of their original brilliancy, are still of great value. On the whole, however, it was found more practical not to fix at all, but to examine a very large number of preparations in the fresh state. A number of diagrams of the ganglia similar to the ground plan of fig. 1) were traced, and into one of these the results of a preparation were drawn. In this way from fifteen to twenty preparations could be made, and their results recorded, in a day. Not only is the number of preparations made greater, but the results obtained are more numerous than if the preparations were fixed, for in order to obtain good permanent preparations it is essential to stop the staining process when it is at its best. If, however, the embryo be allowed to remain in the blue solution, although the colour in most of the elements fades, individual fibres, and especially fresh cells, may continue to stain, and the results thus obtained are often the most valuable.

In dealing with the results obtained by methylene-blue staining, it must be always borne in mind that one can never be quite sure that the whole of the element has taken up the blue. With this reservation, the results to be recorded, which have been obtained after examining many hundreds of preparations, are those only which I regard as practically certain.

More doubtful points will be reserved for further investigation and a future communication.

Embryos at various stages of development have been used, from the time when the eye-pigment first becomes visible until the time of hatching. An element which has once stained at any particular stage is found in practically the same condition at all later stages, excepting that the finer branches become more numerous, and, although the results as given all apply to late embryos, they have been obtained from embryos at different stages. For instance, in tracing certain fibres, which travel the whole length of the cord, although they can be readily recognised in late stages, they have only been actually traced throughout their entire length in much earlier ones. As a general rule, a fibre is most easy to trace through its whole length at the earliest stage at which it will stain.

In the lobster embryo, as in the embryos of other Decapod Crustacea, the thoracic ganglia are fused together into one mass (figs. 1—4), which is united to the brain by a very short commissure (fig. 1, *com.*). At this stage the whole of the commissure which exists is the portion which in the adult lies between the commissural ganglia, from which the stomatogastric nervous system arises, and the first thoracic ganglion, the stomatogastric commissural ganglia (fig. 1, *st. com. gang.*) being now immediately connected with the ganglia from which Antennæ II are innervated (fig. 1, *Ant.* II), and forming part of the brain. The posterior portion of the brain of one side is connected with that of the opposite side by a transverse bridge (*tr. br.*), which lies immediately behind the œsophagus, and which in the adult lies behind the stomatogastric commissural ganglia. Eleven ganglia may be recognised in the fused mass in the thorax. Of these the first six go to form the anterior thoracic ganglion of the adult. In the present paper, for the sake of clearness, the ganglia will be distinguished as Th. I—XI. The ganglion cells of each of these eleven ganglia are arranged in four masses (blue in fig. 1), two lateral and two median, a median dorsal and a median ventral mass, one of the

latter only being shown in the figure. The spaces between the ganglion cells (left white in fig. 1) are occupied by masses of nerve-fibre, the "punkt-substance" of Leydig, or to adopt the more appropriate name suggested by His,[1] the neuropile.

When, shortly after the hatching of the larva, the thoracic ganglia separate, the median masses of ganglion cells of the embryo divide transversely, the anterior portion going to one ganglion, the posterior to the ganglion immediately behind it. In fig. 1 the dotted line between Th. VI and Th. VII represents the line of this division.

In the abdomen the six ganglia are separate in the embryo, as in the adult.

In the following description a ganglion cell, together with the fibre springing from it, will be termed a nerve element. These elements may be divided into three main groups:

I. Elements which lie entirely in the ganglionic chain, and which must be supposed to serve the purpose of co-ordinating the action of its various parts.

II. Elements which consist of a ganglion cell in the cord, and a fibre which runs out at a lateral nerve-root. Some at least of these elements, possibly all, are connected with muscles, and are motor elements.

III. Sensory elements, consisting of cells outside the central ganglionic chain and fibres running from them to a ganglion.

I. Co-ordinating Elements. (Figs. 2—4.)

These elements may be divided into four classes:

A. Elements (fig. 2) made up of a cell in the brain or one of the ganglia, and a fibre which runs posteriorly to the end of the cord, giving off in most cases collateral branches to the neuropile in each ganglion through which it passes.

B. Elements (fig. 3) made up of a cell in one of the ganglia

[1] His, "Histogenese und Zusammenhang der Nervenelemente," 'Archiv Anat. u. Entwickelungsgesch. Anat. Abt.,' Supp. Bd., 1890.

of the cord, giving off a fibre which runs anteriorly to the brain.

C. Elements (fig. 4 red) made up of a cell in one ganglion, and a fibre which runs posteriorly and ends in the next ganglion of the cord.

D. Elements (fig. 4 blue) made up of a cell in one of the ganglia of the cord and a fibre which runs anteriorly, giving off collateral branches in the next ganglion, and ending in the next ganglion but one.

A.

These elements are represented in fig. 2. In this figure only cells of the left side have been drawn, but exactly similar elements exist starting from cells on the right side. The figures 1—4 are necessarily somewhat diagrammatic, but in almost all cases the individual elements are drawn from actual preparations, and I have endeavoured to make the diagrams represent as nearly as possible the actual appearance of preparations.

The elements of this class, for reasons to be explained, must be regarded as only placed provisionally in Group I. It may be necessary subsequently to place them in a group by themselves. Two kinds of A elements may be distinguished—(*a*) those whose fibres decussate (blue in fig. 2), and (*b*) those whose fibres pass down on the same side of the cord (red in fig. 2).

Staining of the following elements of this class has been obtained:—

A (a) Br.—A pair of elements each consisting of a large cell on the ventral surface of the brain, from which a moderately thick fibre at first runs forwards and upwards to the dorsal surface. After turning outwards the fibre runs backwards to a point immediately in front of the œsophagus, where it passes across to the other side and runs down the ganglionic cord. On entering the first thoracic ganglion the fibre becomes very broad, having a diameter many times greater than that of any other fibre in the body, and, maintaining this exceptional size,

runs down the cord to the sixth abdominal ganglion. Here the fibre divides into several branches (fig. 5, A (a) Br), but I have never obtained complete staining of these.

According to Retzius,[1] in the adult Astacus the branches of these fibres pass directly into the nerves which leave the posterior end of the ganglion. If this be the case, the elements must be placed in a class by themselves, as they serve the purpose of putting some organ at the posterior end of the abdomen into direct communication with the brain. This is rendered more probable by the fact that in their course down the ganglionic cord the fibres give off no collateral branches, or at any rate none have ever stained, and I believe none to exist. In the brain, however, a few branches go to the neuropile (fig. 2), the most important being at the angles of decussation. These fibres, both in their narrow portion in the brain and in the broad portion in the thorax and abdomen, often, under the influence of the reagent or from some other cause, assume the beaded form so frequently observed in nerve-fibres.

This pair of elements evidently corresponds to the pair of so-called giant fibres in the adult. The two fibres stain very readily in embryos at all stages, but the cells are a little more difficult to demonstrate. I have, however, traced the fibres into them with absolute certainty on so many occasions that there can be no doubt as to their position and significance. They are often best seen by examining the brain, after the staining is complete, from the ventral surface. Fig. 6 represents such a view.

A (a) Ant II.—This element commences with a cell in the ganglion of the second antenna. After leaving the cell the fibre gives off two stout branches to the neuropile, and then passes through the transverse bridge behind the œsophagus to the opposite side. Here it turns upwards, gives off a branch to the neuropile of the brain, and then turning again downwards, travels along the ganglionic cord.

This fibre has been traced with certainty as far as Abd. 5,

[1] Retzius, "Zur Kenntniss des nervensystems der Crustaceen," 'Biol. Untersuch.,' neue Folge i, 1890.

but as it showed no sign of breaking up or ending there, it probably goes to Abd. 6. This is rendered almost certain from the fact that the element agrees in other respects with the members of the series now being described, which have been actually traced all the way. On its way down the cord, the fibre gives off collateral branches to the neuropile of the different ganglia.

A (a) Th. I.—The cell of this element lies anteriorly in the lateral ganglionic mass of Th. I. The fibre gives rise to a figure of very characteristic shape in Th. I and II, sending off a peculiar branch, which passes downwards on the same side as that on which the cell is situated as far as Th. II, where it turns inwards towards the centre of that ganglion. The main fibre after passing to the opposite side turns down the cord, and has been traced to Abd. 6. The actual ending in Abd. 6 has never stained. The fibre gives off collateral branches in the ganglia through which it passes.

A (a) Th. II.—The cell lies at about the centre of the lateral mass of ganglion cells. The fibre gives off an upward and downward branch to the neuropile of the same side, then passes across to the opposite side, and runs down the cord. It gives off collateral branches, and has been traced to Abd. 6.

A (a′) Th. II.—This is an element starting from a cell in the ventral median mass of ganglion cells of Th. II. The fibre passes upwards and outwards to Th. I, where it decussates and then runs down the cord on the opposite side. It has been traced to the end of the thorax, but does not appear to stop there. It has collaterals, at least during the upper part of its course.

$\left.\begin{array}{l}\text{A (a) Th. III.}\\ \text{A (a) Th. V.}\end{array}\right\}$—These fibres are similar in their relations to A (a) Th. II, but they have only been actually traced to the end of the thorax.

It may be explained here that the great difficulty in tracing fibres from the thorax to the abdomen of lobster embryos is due to the abdominal flexure. It is impossible to straighten out the abdomen without such injury as interferes with the staining, or causes it to disappear. Hence it is only when

one or at most two fibres are stained upon the same side of the cord that it is possible to trace them with certainty through their whole course. This, however, does not apply to the giant fibres (A (a) Br), which can always be easily recognised.

A (b) Br.—This element starts with a cell of moderate size on the ventral surface of the brain immediately anterior to the large cell of the giant fibre (A (a) Br). The fibre passes first forwards and upwards, giving off numerous branches to the anterior lobes of the brain on both sides, and then backwards through the brain and down the ganglionic cord of the same side to the sixth abdominal ganglion. It give off collateral branches to the neuropile of the ganglia through which it passes.

A (b) Th. III.—The cell of this element lies on the inner ventral border of the lateral mass of ganglion cells of Th. III. The fibre runs forwards and inwards, and then forwards and outwards to Th. II. After giving off a branch which enters Th. I it turns downwards on the same side of the cord, sending off a stout branch in Th. III, and has been traced to the end of the thorax. It gives off collateral branches during its whole course.

A (b) Th. IV.—The cell lies in the median ventral mass of ganglion cells, but it is difficult to decide whether it should be considered as belonging to Th. III or Th. IV. The fibre passes forwards and outwards to a point in Th. III, where it gives off a stout transverse arm, which runs to the neuropile of the opposite side and there bifurcates. The main fibre turns downwards, gives off a branch which runs forwards to Th. II, and then runs down the cord on the same side as that on which the cell is situated. It has been traced to the end of the thorax, and gives off numerous collateral branches.

B.

These elements are represented in fig. 3. In all cases similar elements exist upon both sides of the cord, although, for the sake of clearness, only one is sometimes inserted. The elements consist of fibres starting from a cell in a thoracic ganglion and running forwards to the brain. Of this group the following have stained :

B Th. I.—The cell lies in the ventral median mass of ganglion cells. The fibre runs forwards and outwards, and then decussates. After reaching the opposite side it goes forwards to the brain. It has been traced as far as the cross in the figure. No collaterals have been observed after the fibre leaves Th. I. A similar element occurs on the opposite side.

B Th. II.—Cell lies in lateral mass. Fibre gives off a large arborescent branch in Th. II, and one also which passes downwards to Th. III. It then runs across to the opposite side, turns forwards, and goes to the brain. No collaterals have been observed, with the exception of those figured.

This element generally forms a conspicuous object when stained, on account of the comparative stoutness of the fibre at the part where the branches occur, and the richness of the arborescence.

B Th. V.
B Th. VIII. —These elements will be considered together, as they appear to be very intimately associated, ending in the same part of the brain, and being generally found stained in the same preparations. The cell of each element lies in the anterior portion of the lateral ganglionic mass. Soon after entering the neuropile the fibre gives off two branches, one running forwards and breaking up in the hinder portion of the ganglion immediately anterior, whilst the other runs backwards and breaks up in that immediately posterior. The main fibre turns inwards, crosses its fellow of the opposite side, and then bends forwards, running close to the median ganglionic cells, until it enters the brain. In the brain the fibre continues to run forwards, giving off many branches, and ends at about the level of the nauplius eye. These fibres have not been observed to give off collaterals during their course through the thorax.

The two pairs of elements just described very frequently stain with methylene blue, and the characteristic figures produced by their decussation are very useful landmarks in preparations.

B Th. VI.—This element resembles B Th. I more nearly than B Th. II, V, or VIII. The cell lies in the ventral median mass of ganglion cells. The fibre curves outwards and backwards,

and then forwards and inwards, gives off a branch to the neuropile of the same side, and then passes across to the other side. It runs forwards to the brain along the outer border of the neuropile, and breaks up at a point nearly as far forwards as the terminations of Th. V and VIII, but somewhat lateral to them.

No collateral branches have been observed in ganglia other than that in which the element originates.

C.

These elements are best observed in the posterior ganglia of the thorax of very late embryos or young larvæ. Their existence in practically the same condition can, however, be made out very much earlier, in fact soon after the eye-pigment begins to deposit. They are represented in fig. 4 in red, whilst fig. 7 is a drawing of one of these elements made from a fresh preparation. Several of them are also shown in fig. 8, which is drawn directly from a preparation fixed in ammonium picrate.

These elements have been clearly demonstrated in each segment between Th. VI and Th. XI, and there is evidence of their existence in the more anterior segments. Starting from a cell in the anterior portion of the lateral mass of ganglion cells, the fibre passes inwards and backwards for a short distance, and then turns till it runs almost directly backwards, giving off to the neuropile numerous branches, which are themselves arborescent. After a short backward course it again turns inwards, and finally runs directly backwards between the fibre of series D (blue in fig. 4) and the median ganglionic mass. Each element ends in a tuft of fibres (figs. 4 and 7), which lies at the posterior end of the ganglion next to that in which the element originates, and immediately opposite the terminal tuft of one of the D elements.

D.

These elements are also best observed in very late embryos. They appear to be intimately associated with those of group C, and generally stain in the same preparations. They are repre-

sented in blue in fig. 4, and are also seen in fig. 8, which is drawn from a fixed preparation. This latter figure illustrates the extent to which the systems C and D will stain in a favourable preparation. The elements can be recognised in six segments, although in some cases the cell has not stained. The cells of elements D lie in the posterior portion of the lateral ganglionic mass. The fibre passes forwards and inwards through the neuropile, giving off numerous arborescent branches to the latter. On entering the next ganglion in front, the fibre has reached the outer border of the median ganglionic mass, and after giving off a little tuft of branches immediately in front of the tuft in which one of the elements C ends, it pursues a direct anterior course, ending in a tuft of branches in the ganglion next but one to that in which it started. This terminal tuft lies opposite the terminal tuft of one of the C (red) elements, and immediately behind the lateral tuft of the D (blue) element of the next ganglion. These relations will, I think, be more readily understood from a study of fig. 4 than by any further description. It should, however, be stated that the three tufts standing opposite each other are at exactly the same level in the cord, being all three in the focus of the microscope at the same time. The fine fibres of which they are composed are often obscured owing to the rapidity with which they assume the beaded condition.

II. Motor Elements.

Under this head will be described those elements which consist of a cell in the ganglionic cord, giving off a fibre which, after sending arborescent branches to the neuropile, passes out from the cord by one of the nerve-roots. Many of these elements (not improbably all of them) are motor, and in some cases I have been able to trace the fibre from the cell, through its whole course, until it breaks up on a muscle. Such a case is represented in fig. 9, which was drawn from a preparation preserved in ammonium picrate.[1]

[1] The slight break in the fibre, which was not present when the preparation was fresh, is, even on an examination of the preserved preparation, due to

Fig. 1 contains types of most of the elements of this kind which have stained. In this figure the general course of the nerves springing from the ganglionic cord is indicated. In the more posterior ganglia (Th. IV—VIII) it will be observed that two nerve-roots exist, one anterior (*ant. n. r.*) and one posterior (*post. n. r.*). Fibres passing out at the anterior root go for the most part to the limbs, whilst those passing out at the posterior root supply the wall of the body, and their general distribution is indicated. The anterior root is in reality a double root, the two halves separating at a later stage. In Th. II and III this separation has already taken place. In fig. 1, for the sake of clearness, those elements which originate in cells of the central ganglionic mass are coloured red, whilst those having their origin in the lateral mass are blue. Each of the ganglia Th. VI to Th. IX contains exactly similar elements. One element of each kind which has stained has been drawn upon both sides in Th. VIII, whilst to render them clearer only one element of each colour has been inserted in Th. VI, VII, and IX.

The lettering will be continuous with that of the elements already described.

E. Type: the Blue Element of fig. 1 in Th. VI and VII.

This element starts from a cell in the anterior portion of the lateral mass of cells. The fibre runs first inwards, and then curves downwards and outwards, leaving the cord by the anterior nerve-root. The fibre gives off three main branches to the neuropile, which gives a very characteristic trident shape to this portion of the element. In late stages the three main branches give off numerous smaller ones, but these have been omitted in fig. 1 for the sake of clearness.

Two or even three elements of this type are sometimes stained on the same side of a ganglion at one time.

The element has stained in Th. III, Th. V—XI. In fig. 1, E Th. III, Th. V—VIII are inserted.

an accident in putting it up. The drawing has, however, been made from this preparation, in preference to others, on account of the whole being more clear and satisfactory.

The element E. Ant. 2 resembles in some points the members of this group.

F. Type: the blue element in Th. IX, fig. 1.

This element starts from a cell in the lateral mass, which lies very near the ventral surface. The fibre passes backwards and inwards, and then suddenly turns and runs forwards and outwards until it reaches the level of the anterior nerve-root, when it turns backwards and outwards and so leaves the cord. At the points where the fibre turns, branches are given off to the neuropile. Only one element of this kind has been observed to stain in the same ganglion at one time.

The element has stained in Th. V—IX. In fig. 1, F Th. V, Th. VIII, Th. IX are inserted.

The element F Th. I may also belong to this group.

G. Type: the red element of Th. VI in fig. 1.

This element starts from a cell in the median mass of ganglion cells.[1] From the cell the fibre passes outwards, and after a somewhat curved course leaves the cord by the anterior root. It gives off two main branches to the neuropile, one of which gives off a third, the whole producing a figure somewhat resembling the trident figure of element E. Two or three elements of this type may stain on the same side of one ganglion.

The element has stained in Th. II, III, VII—IX. In fig. 1 it is inserted in Th. II, III, VI, VIII, IX.

G Th. III is an element which stains in almost every preparation of young stages, and forms a useful landmark in the cord.

H. Type: the red element in Th. X.

Originates from a cell in the median mass, from which the

[1] As has already been stated (p. 5), the median masses of cells in the embryo divide transversely soon after the larva is hatched, the anterior portion going to one ganglion, the posterior portion to the ganglion behind it. The division takes place between the two groups of red cells in fig. 1, Th. VI and VII, at the level of the dotted line.

fibre takes a slightly curved course outwards and downwards, to pass from the cord by the anterior root. It gives off three or four small branches to the neuropile. The element stained in Th. V—X. Inserted in fig. 1 in Th. V, VII, VIII, and X.

J. Type: the red element passing through the posterior root in Th. VII.

The fibre of this element has a somewhat curious course. It starts from a very small cell in the median mass, runs for some distance outwards, and then takes a circular course through the neuropile, forming a complete loop, after which it passes outwards to the posterior root. From the upper margin of the loop three branches are given off, whilst from its lateral side a straight arm passes inwards and meets a similar arm from the opposite side. A direct fusion of the two arms has, however, never been observed. This element has stained in Th. VII—IX, and is inserted in each case in the figure.

K.

This element has been satisfactorily demonstrated up to the present only in Th. III. The cell lies in the median ventral mass, and from it the fibre passes outwards for a considerable distance, then suddenly turns and runs inward until it crosses its fellow of the opposite side, from which point it continues its former direction till it passes out at the posterior root of the ganglion, on the opposite side to that upon which the cell lies. This element differs, therefore, from the elements previously described in the fact that fibres of opposite sides decussate.

L.

This is an element in Th. I, and is coloured red in the figure. The cell lies near the median mass. The fibre passes backwards and slightly outwards, then turns upwards and passes out at the anterior root. A branch is given off at the point where the fibre turns, which soon bifurcates, one branch running backwards, whilst the second runs transversely to the opposite side of the ganglion.

III. Sensory Elements.

These are nerve elements in which the cell lies outside the ganglionic cord.

M.

Up to the present I have only been able to obtain satisfactory staining of such elements in lobster embryos in the abdomen. If the ganglionic cord in the thorax be cut across at any point behind the œsophagus, numerous longitudinal fibres take up the methylene blue, and many of these continue to stain until, on turning the embryo over, they may be seen to pass into the abdomen. In some preparations some such fibres are seen to pass out at the lateral nerves of the abdominal ganglia, and may be traced backwards and upwards to the dorsal surface of the abdomen, where they end in cells similar to those described by Lenhossék[1] and Retzius[2] in the earthworm, and by Retzius[3] in Polychætes and Molluscs.

These cells vary somewhat in shape. Two of them are represented in fig. 10. The cell itself is generally spindle-shaped, the distal end either running out and ending in a sharp fibre (fig. 10, *b*), or being flattened out as in fig. 10 (*a*). In other cases the distal end of the cell appears rounded, as in the lower cell of fig. 11, but this may be due to incomplete staining.

The fibre arising from the proximal end of the cell, which lies on the dorsal surface of the abdomen, is moderately fine, and as previously stated passes forwards and downwards to the nerve cord. The cell generally lies vertically over the ganglion behind that into which the fibre enters (fig. 11). Within the ganglion the fibre bifurcates, forming a Y-shaped figure, one arm of which passes forwards and the other backwards. As to the endings of these fibres, I regret that I can at present

[1] Lenhossék, "Ursprung, Verlauf, und Endigung der sensibeln nervenfasern bei Lumbricus," 'Arch. mikr. Anat.,' 39, 1892.

[2] Retzius, "Das nervensystem der Lumbricinen," 'Biol. Untersuch.,' neue Folge iii, 1892.

[3] Retzius, "Das nervensystem der Lumbricinen," 'Biol. Untersuch.,' neue Folge, iv, 1892.

make no definite statement. When the fibres are stained in two or three successive ganglia, as is generally the case, the appearance presented is that given in fig. 11. The fibres from different ganglia run very close together, and it is impossible to differentiate them individually. In a few cases, however, the fibre of only one ganglion has stained. The most interesting of these is represented in fig. 12, A. The abdomen was first examined at a somewhat early stage of the staining, when in the ganglion of Abd. II the Y-shaped bifurcation was coloured. The anterior arm of the Y was actually traced as far as the posterior end of Th. XI (last thoracic ganglion), but could not be followed further on account of the flexure. The posterior arm was traced through Abd. III and through Abd. IV, but the staining had ceased before Abd. V was reached. After the staining had proceeded for some time longer, the appearance represented by Abd. II was that shown in fig. 12, B, and the corresponding fibres in the other abdominal ganglia were commencing to stain.

As these elements often stain when the ganglionic cord is cut across at the level of the œsophagus, and when there is no visible wound behind that point, it seems possible that they may run forwards as far as the brain, although this is at variance with the conclusions arrived at by Lenhossék and Retzius for similar fibres in other Invertebrates.

I may here mention that similar cells to those just described I have found in large numbers on the wall of the œsophagus of Astacus.

N.

In Th. I and Th. II there are two nerve-endings in connection with which no cell has ever stained in the cord, although the fibres stain with very great frequency. It is not unlikely that these are sensory nerves, whose cells lie outside the cord. That of Th. I, which enters at the posterior root, is figured in fig. 13, whilst that of Th. II is inserted in fig. 1 at N. The latter is the more striking of the two on account of the fact that it not only branches in Th. II, but also sends stout

branches which arboresce in Th. I and in Th. III. The fibre therefore influences three adjacent ganglia.

I have made numerous observations of certain other nerve-endings in the thoracic ganglia, which are very possibly the endings of sensory nerve-fibres, but the account which I could give of these is at present not sufficiently complete to make it worth while describing them here, and I prefer to reserve them for future investigation.

Theoretical.

Without entering into a general discussion, which will be more suitable after the investigations have been continued to a further stage, I shall now endeavour to draw attention to some points of interest in the results described above.

In the first place, the elements C and D (fig. 4), which form what may be termed the short internal connections of the cord, will be considered. I am of course aware that there is a possibility that this arrangement of fibres is purely embryonic, and has not yet reached the active condition. This view, however, appears to me to be improbable, firstly on account of the fact that there is practically no change in the arrangement from quite early embryos, in which the eye-pigment has just begun to deposit, to the oldest larvæ (about one week) which I have been able to examine; and secondly, because the elements take up the methylene blue in a way which, according to present experience, only active nervous tissue does.

At the outset, the question arises as to what is the significance of the three tufts of fibres which stand opposite to each other at the point where each element ends, and of the lateral branches, which both elements give off to the neuropile, where they cross. My observations agree entirely with those of Retzius, Kölliker, and the majority of recent investigators, in the fact that I have never, here or elsewhere, been able to observe anastomosis of the fibres of different elements. There can, however, be little doubt that the view now commonly held that it is by means of the finer branches that the nervous energy passes from one element to another is the

true one, although in what way this takes place remains unknown. The constant relative position of these three tufts of fibres would seem to be inexplicable upon any other assumption, and it appears at least worth while to make the suggestion that the nervous energy resembles a static electrical charge, in the fact that the discharge takes place most readily through points. Wherever the methods of Ehrlich and Golgi have been applied to demonstrate the endings of nerve-elements, the breaking up of the fibre into finer and finer branches which end freely has been shown to occur, and the suggestion is that it is by means of these fine branches that the nervous discharge takes place.

On the view suggested, each nerve-element resembles an electrical condenser capable of charging itself, and being suddenly discharged by an appropriate stimulus. The tufts of fibres at the ends of the elements C and D (fig. 4) would be comparable to the "brushes" of an electrical machine. In the same way we should suppose that the nervous energy passes from one element to some other element by means of the numerous branches given off to the neuropile.

Now it must be borne in mind that the elements represented in fig. 1, some of which at any rate we know to be motor elements (cf. p. and fig. 9), also send off numerous branches to the neuropile, which interlace with the branches of the elements C and D. One such element has been inserted in black in Th. VIII (fig. 4). Although the speculation has perhaps little value, it is at least interesting to consider what would happen upon the suggested theory, supposing one of the elements to be in any way stimulated. Imagine, for instance, the element D Th. VIII to be caused to discharge, either by an impulse received from a sensory nerve-ending, or by an impulse coming along a fibre from the brain. The main discharge would, we must suppose, pass into such an element as E, and so along the motor nerve to the muscle. A portion, however, would pass along the element D to the lateral tuft, from which it might pass to the terminal tuft of the element D of Th. IX and, we may suppose, cause this element to discharge. Another

portion would pass on to the terminal tuft of Th. VIII D, and would discharge Th. VII D. In this way the discharge would pass right along one side of the thorax, and the particular motor fibre concerned would be stimulated in each segment, the stimulus being conveyed in its turn to the muscles. If we suppose the fibres of the element C to discharge into those of D at the point where the fibres cross, the use of this series of elements is difficult to understand, as the elements D are by themselves capable of discharging each segment. There is, however, an alternative supposition. It may be that the branches of C influence not either D or E, but some other motor element, say F. Then by means of the terminal tufts of the D (blue) elements the C (red) elements would all be discharged, and they in their turn would stimulate all the F elements, which would cause the particular muscle innervated by F to discharge. Thus by the stimulation of the element D Th. VIII the two muscles innervated by elements E and F in each segment, upon one side of the thorax, would be made to contract.

We now pass to the elements A and B, by means of which the brain and anterior ganglia are connected with the remaining ganglia of the cord (elements A, fig. 2), and a particular ganglion is put into direct communication with the brain (elements B, fig. 3). The fact that the fibres of elements A send out collateral branches into the neuropile of each ganglion indicates that they control some element which also has branches in that particular ganglion, and the suggestion would be that by their means a series of elements are stimulated all along the body by an impulse from the brain. On the other hand, by means of elements B a particular ganglion would be placed in more direct communication with the brain. This communication will be independent or correlated with a stimulus to (or from) all the ganglia through which the fibre passes, according to whether the absence of collaterals is the true condition of the element, or is due merely to imperfect staining.

With regard to the giant fibres (A (a) Br) a good deal

also depends upon whether or not the absence of collaterals represents the true condition. This is almost certainly the case on account of the ease and frequency with which these elements stain, and the readiness with which their branches in the brain are demonstrated. It will be remembered, too, that, according to Retzius, the branches into which the fibres divide in the last abdominal ganglion pass out through the nerves of that ganglion, and it therefore seems probable that they serve the purpose of putting some organ into direct communication with the brain. It may be that these branches go directly to the muscles which control the tail fin, so that the steering apparatus of the animal is under the direct control of the brain. This, at any rate, is the most obvious suggestion.

It is of course possible that the other elements of the class A serve a similar purpose, but the fact that they have collateral branches in each ganglion seems to me to be opposed to this view.

The above remarks are intended merely as an indication of the nature of the problems suggested by the observations recorded in the previous part of the paper, problems which can only be finally solved by means of physiological research, for which research, however, an accurate knowledge of anatomical details is an essential preliminary.

EXPLANATION OF PLATES 35 and 36,

Illustrating Mr. Edgar J. Allen's paper on "Some Nerve Elements of the Embryonic Lobster."

Fig. 1.—Brain and thoracic ganglia of Homarus embryo. Motor elements. *œs.* Œsophagus. *st. com. gang.* Commissural ganglion from which stomatogastric nerves arise. *tr. br.* Transverse bridge behind œsophagus. *com.* Œsophageal commissure. *ant. n. r.* Anterior nerve-root. *post. n. r.*

Posterior nerve-root. *Ant. II.* Ganglion of Antenna II. *Th. I—X.* Thoracic ganglia. *I—VI.* Form anterior ganglion of adult. *E—N.* Elements, chiefly motor. See pp. 495—499. Somewhat diagrammatic.

FIG. 2.—Brain and thoracic ganglia of Homarus embryo. A. Elements. Fibres run from cell in anterior ganglion, and pass down ganglionic cord. For individual elements see pp. 488—491.

FIG. 3.—Ditto, B elements. Fibres run from cell in ganglion forwards to brain (see pp. 491—493).

FIG. 4.—Ditto, C and D elements. *C.* Fibres run from cell backwards and end in next ganglion. *D.* Fibres run from cell forwards and end in next ganglion but one. E. Motor element. (See pp. 493, 494).

FIG. 5.—Branching of giant fibres in sixth abdominal ganglion. A (a) Br. Giant fibre.

FIG. 6.—View of brain of Homarus embryo from the ventral surface. A (a) Br. Cell in which giant fibre originates.

FIG. 7.—Element C. Camera drawing from fresh preparation. Late embryo. × 250.

FIG. 8.—Posterior thoracic ganglia (Th. VI—Th. XI) of Homarus embryo. Elements C and D stained. Camera drawing from preparation fixed in ammonium picrate. × 100.

FIG. 9.—Posterior thoracic ganglion (Th. XI), showing nerve-cell (*n. c.*) and fibre going to muscle (*musc.*). Camera drawing from preparation fixed in ammonium picrate. × 250.

FIG. 10.—Sensory cells in ectoderm of dorsal surface of abdomen of Homarus embryo.

FIG. 11.—Three abdominal ganglia (Abd. II—IV) of Homarus embryo, showing sensory elements M.

FIG. 12.—*A.* Second abdominal ganglion (Abd. II) of Homarus embryo showing bifurcation of fibre of sensory element M. *B.* Ditto, at a later stage of staining.

FIG. 13.—Nerve-ending in Th. I.

Studies on the Nervous System of Crustacea.

By

Edgar J. Allen, B.Sc.Lond.

With Plates 37 and 38.

II.—The Stomatogastric System of Astacus and Homarus.
III.—On the Beading of Nerve-fibres and on End Swellings.

II.

With a view to making myself acquainted with the use of Ehrlich's methylene blue method, in order to study the structure of the nervous system of the larvæ and embryos of Decapod Crustacea, I made preliminary trials upon the stomatogastric nervous system of Astacus. As several points of interest appeared, I carried the observations further than I had intended, and I now propose to give some account of them, especially as I am able to supplement them in one or two particulars by observations which I have made during my later work on the embryos of Homarus.

The greater portion of the research recorded here was carried out in the zoological laboratory at University College, and my thanks are due to Professor Weldon for the help and advice which he has given.

Method.—My attention was chiefly directed to the study of that portion of the stomatogastric system which puts it into communication with the central nervous system of the animal. The following mode of procedure was adopted:—The animal, after being killed with chloroform, was opened from the dorsal

surface, the anterior gastric muscles were carefully cut through, as much of the green gland as possible removed with forceps, and the brain freed in front from the carapace. The whole of the head in front of the mouth was then cut off with a pair of stout scissors, and the anterior thoracic ganglion exposed from the ventral surface. When this has been done the whole stomach can be removed with the œsophageal nerve-ring attached. In some cases the thoracic ganglion was not dissected out, the commissures being simply cut across as far back as possible. The stomach thus removed from the animal was then placed in normal salt solution, and its anterior face, with the œsophagus and the anterior gastric muscles attached, cut off. After the œsophagus had been slit longitudinally along its posterior wall, the whole piece thus obtained was spread out on a slide with the nerve-ring lying uppermost. The preparation was then covered with a dilute solution of methylene blue in normal salt solution. In order to keep the tissue properly covered, it is an advantage to have a glass or metal cell attached to the slide. The strength of methylene blue found most useful was from 1 : 50,000 to 1 : 10,000. It is often good to start with the more dilute solution, and gradually add the stronger as the staining proceeds. In cold weather the slide should be kept warm; indeed, the staining always takes place more rapidly at a temperature of 25°—30° C.

One great advantage of this method, due largely to Biedermann[1] and Apáthy,[2] over the original method of Ehrlich, lies in the fact that the object can be examined with the microscope from time to time, and the staining process watched. When the staining is at its best it may be fixed by placing the tissue in a solution of ammonium picrate containing excess of ammonium carbonate (Apáthy), and, after a few hours, mounting in glycerine mixed with an equal volume of the fixing solution To obtain good preparations a great deal depends

[1] Biedermann, "Über den Ursprung und die Endigungsweise der Nerven in den Ganglien wirbelloser Thiere," 'Jena. Zeitschr.,' Bd. xxv, 1891.

[2] Apáthy, "Erfahrung in der Behandlung des Nervensystems für histologische Zwecke," 'Zeitsch. wiss. Mikr.,' Bd. ix, 1892.

upon judging properly the moment to stop the staining process. If the latter be allowed to continue for too long a time, the nervous elements lose their colour, and a diffuse staining of other tissues takes place.

It is necessary to make a large number of preparations to obtain satisfactory results, and care must be taken not to pull the tissue about very much in getting it ready. It must also be so arranged that all the nerves lie freely exposed to the methylene blue solution, and not covered by other tissues. If these precautions are attended to, very beautiful results can be obtained.

The diagram, fig. 1, represents much the appearance of a good methylene blue preparation, and the individual elements there recorded are taken from actual preparations. The figure represents the nerve-ring turned through nearly a right angle until it comes to lie upon the anterior surface of the œsophagus, as it will do in preparations made as described above. From the brain (*Br.*) the two œsophageal commissures run down upon either side, and contain numerous stained fibres which often are beaded in various ways. This beading, which will be afterwards discussed in more detail, is not the natural condition of the fibre, and can give rise to a variety of appearances, some of the more typical being recorded in the commissures drawn in the figure.

About one third of the way down the commissure is the ganglionic swelling (*com. gang.*) from which the nerves of the stomatogastric system spring. Behind this swelling lies the transverse bridge (*tr. br.*), which runs from one commissure to the other, and in the natural position of the parts is situated immediately behind the œsophagus. It is worth noting that all the fibres observed to pass through this transverse cord come down the commissures, a few possibly from the commissural ganglia, the majority from the brain.

From each of the commissural ganglia two nerves spring, which unite with their fellows of the opposite side in what is practically a somewhat diffuse ganglion, which lies in the middle of the anterior surface of the œsophagus, and will be

termed the œsophageal ganglion (*œs. gang.*). From this ganglion the azygos nerve (*azy.*) takes its origin, and runs up the anterior face of the œsophagus and stomach to the ganglion which lies between the anterior gastric muscles. This ganglion will be termed the gastric ganglion (*gast. gang.*, fig. 2). There are thus four ganglia connected with the stomatogastric system—the pair of commissural ganglia, the œsophageal ganglion, the gastric ganglion.

Returning now to the two pairs of nerves which spring from the commissural ganglia, and bearing in mind that in the figure (fig. 1) the brain is supposed to be turned back upon the œsophagus, it will be seen that one of these pairs lies more anterior and ventral (*vent. n.*) (antero-lateral nerve of Huxley's description), the other more posterior and dorsal (*dors. n.*) (medio-lateral nerve, Huxley).[1]

The ventral nerve, after giving off close to its point of origin with the commissural ganglion a small nerve (*a*) which breaks up on the wall of the œsophagus, runs downwards towards the mouth for some distance, and then turns upwards to the œsophageal ganglion. At the point where the nerve turns upwards a downward branch (*b*) is given off, which breaks up and, together with its fellow of the opposite side and a median nerve (*c*) coming from the œsophageal ganglion, forms a large plexus of fibres (*plex.*) at the border of the mouth. An examination of the point where this branch (*b*) takes its origin from the ventral nerve shows that the plexus receives two sets of fibres, some coming from the direction of the œsophageal ganglion, others from that of the commissural ganglion. It is also somewhat curious that most of the fibres which have stained in the median nerve (*c*) running from the œsophageal ganglion to this plexus appear to come, not from the ganglion itself, but through the ventral nerve (*vent. n.*) from the direction of the commissural ganglion. What the meaning of this fact is I do not know.

The ventral nerve (*vent. n.*) itself obtains fibres from various sources. Many of its fibres are seen to enter the commissural

[1] Huxley, 'Anat. Inv.,' p. 286.

ganglia, and there arboresce, as in fig. 1 on the right side. In Astacus, however, I never succeeded in demonstrating the connection of any of these fibres with ganglion cells. Many cells were stained, as in the ganglion on the left side of fig. 1, but their connections could not be made out. In the lobster embryo I was fortunately able to fill up this gap in my previous work. Fig. 2 represents the stomatogastric system of such an embryo, and the element A is seen to start from a cell in the commissural ganglion (which in the embryo forms practically a part of the brain) and enter the ventral nerve.

Other fibres of the ventral nerve come from the œsophageal ganglion. Figs. 3 and 4 represent enlarged views of this ganglion drawn directly from single preparations. Two kinds of cells are found in it, both of which send fibres to the ventral nerve, the one kind being unipolar, the other bipolar. The bipolar cells (figs. 1 and 4, C_1, C_2) are spindle-shaped cells sending off a fibre from each end. One fibre runs upwards to the azygos nerve (*azy.*), the other downwards through one of the ventral nerves. Some of these cells lie in the portion of the ventral nerve which adjoins the ganglion (figs. 1, 4, C_1) rather than in the ganglion itself. The unipolar cells (figs. 1, 3, 4, D, E, M) give off a single branch which, however, generally soon divides, one of the branches bifurcating again almost immediately, so that there are really three fibres having their origin in the one unipolar cell (figs. 3, 4, D_1, D_2, D_3). Of these three fibres, one runs upwards to the azygos nerve (D_1), whilst the other two run downwards through the ventral nerves to the commissural ganglia (D_2, D_3). It is probable that by means of these elements the gastric ganglion and the two commissural ganglia are put into direct communication. In fig. 4 a unipolar cell (E) is drawn, which gives off one branch which does not divide but passes directly into the right anterior nerve. It is not improbable, however, that this is due simply to incomplete staining, and that the element is in reality of the same type as that already described (D).

In fig. 3 is a cell (F) which appears to be closely applied to a single fibre. This probably represents an intermediate stage

between the unipolar and bipolar type of cell. It may be regarded as a bipolar cell in which the two poles have come to lie closely together, or as an unipolar cell the single process of which immediately bifurcates. It is interesting to note that in the lobster embryo all the cells of the œsophageal ganglion (fig. 2, F) which have stained, are of this type.

His[1] has shown that the cells of the spinal ganglia of human embryos are at first bipolar, giving off one nerve process to the cord, the other to peripheral parts. In later stages the body of the cell becomes excentric to the axis passing through the two fibres, and by degrees a single process with a T-shaped fibre is formed. V. Lenhossék[2] has found both bipolar cells and unipolar cells with a T-shaped fibre in Pristiurus embryos, and discusses the transition of one form into the other. Ramon[3] also notes the fact that in embryonic birds the cells of the spinal ganglia are all bipolar, whereas in adult mammals they are unipolar with a bifurcating fibre.[4]

In addition to those already mentioned, fibres from several other sources enter the anterior nerve. Some fibres pass down from the azygos nerve (hence probably from the gastric ganglion) directly into one or other of the anterior nerves. Such fibres are represented (G) in fig. 3, and they are also inserted in fig. 1. A fibre, which passes from the dorsal nerve of one side to that of the other (fig. 1, H), has also been observed to give off a branch which passes down one of the ventral nerves.

Lastly, the œsophageal ganglion is connected directly with the brain by an anterior median nerve (*ant. med. n.*, figs. 1, 3, 4) which Huxley describes as "the anterior continuation of the azygos nerve."[5] Fibres passing from the brain along this

[1] His, "Histogenese und Zusammenhang der Nervenelemente," 'Arch. Anat. u. Entw. gesch. Anat. Abt.,' Supp. Bd., 1890.

[2] V. Lenhossék, "Beobactungen an den Spinalganglien und den Rückenmark von Pristiurusembryonen," 'Anat. Anz.,' 7, 1892.

[3] Ramon y Cajal, "Sur l'origine et les ramifications des fibres nerveuses de la moelle embryonnaire," 'Anat. Anz.,' 5, 1890.

[4] Compare also Retzius, 'Biol. Untersuch.,' neue Folge iv, 1892.

[5] I have only observed one such nerve (cf. Huxley, 'Anat. Inv.,' p. 287).

nerve bifurcate in the œsophageal ganglion, a branch then passing into each of the ventral nerves (figs. 1 and 3, II). It is probable that in this way the commissural ganglia are placed in direct communication with the brain. As, however, I have not followed one of these fibres individually to the commissural ganglion, there is of course the alternative that it may pass out at the branch (*b*) and enter the plexus (*plex.*) at the border of the mouth.

Passing now to the dorsal nerves (*dors. n.*) arising from the commissural ganglia, I was here again able to complete the observations I had made on Astacus by those on the lobster embryos. In the latter, fibres were often observed starting from cells in the commissural ganglia (fig. 2, B), and after giving off numerous arborescent collateral branches to the neuropile, passing into the dorsal nerve and so to the azygos.

After leaving the commissural ganglion, the dorsal nerve gives off a branch (*d*) which runs upwards on the wall of the œsophagus and soon breaks up into a large number of individual fibres, each one having in its course a moderately large bipolar cell (J, fig. 1). These cells exactly resemble sensory cells described by Retzius[1] in many Polychætes and Molluscs.

As near as I could determine in preparations in which the general tissue was not stained, they lie on the exterior surface of the œsophagus, whilst the distal fibres proceeding from the cells, sometimes after a very long course, end in a much deeper layer, probably on the interior face of the œsophagus. The proximal fibres from these cells all enter the branch (*d*) of the dorsal nerve, and the fibres of this branch enter the commissural ganglion.

A few fibres passing through the branch (*d*) break up on the

[1] Retzius, 'Biol. Untersuch.,' neue Folge iv, 1892: 1. "Das Sensible Nervensystem der Polychäten;" 2. "Das Sensible Nervensystem der Molluscen." Compare also Lenhossék, 'Arch. mikr. Anat.,' 39, 1892, and Retzius, 'Biol. Untersuch.,' neue Folge iii, 1892, for similar cells in Lumbricus.

wall of the œsophagus as at *K* (fig. 1), that is to say, in the typical manner of motor nerve-endings.

At a slightly higher point to that from which the branch above described arises, the dorsal nerve gives off a second branch (*E*), which runs forwards on the œsophagus, and breaks up into a mass of fibres, each of which has a bipolar ganglion-cell in its course (*L*). These cells are confined to two limited areas on the wall of the œsophagus, which may almost be regarded as definite sense-organs. The cells of the first branch (*K*) are much more scattered than these; indeed, they may be found upon all parts of the œsophageal wall. These cells of the second branch are similar in shape to those of the first, but are much smaller, and the fibres springing from their distal ends are shorter. Their fibres can be readily traced through the wall of the œsophagus to its inner surface, where they appear to end. From the position of these elements it is not unlikely that they form organs of taste.

After giving off these two branches, the dorsal nerves unite with each other and with the œsophageal ganglion, or rather unite to help to form the œsophageal ganglion, for it would seem that the whole tract of nervous tissue where the ventral and dorsal nerves unite should be included under that name. The ventral portion alone contains ganglion-cells, but in the dorsal portion the fibres give off numerous collateral branches (fig. 1, *neu.*), forming a small neuropile, so that this part must also be regarded as belonging to the ganglion.

Several kinds of fibres enter the dorsal nerves from the œsophageal ganglion. Some fibres spring directly from cells in the ganglion, as at fig. 3 M, whilst others take their origin from fibres which come down the azygos nerve, bifurcate in the upper part of the œsophageal ganglion, and send one branch down each dorsal nerve (figs. 1—3, N). One such fibre in the lobster embryo (fig. 2, N) has been traced to a bipolar ganglion-cell which lies at the anterior end of the gastric ganglion.

Some fibres pass directly from the azygos nerve into one of the dorsal nerves (fig. 3, O).

The azygos nerve itself, after leaving the œsophageal gan-

glion, passes up the anterior face of the stomach to the gastric ganglion. This ganglion is spindle-shaped (fig. 2, *gast. gang.*), and from the opposite end of the spindle to that at which the azygos enters a stout nerve is given off, which bifurcates on the dorsal surface of the stomach (fig. 2). The gastric ganglion of Astacus is enclosed in a connective-tissue sheath, which can with care be removed. When this is done, the large unipolar cells can be seen protruding on either side, each invested in a nucleated sheath. One such cell with its sheath is represented in fig. 5. The central portion of the ganglion is occupied by a mass of neuropile made up of the arborescent branches springing from the processes of the ganglion cells, and the arborescent ends of fibres which enter the ganglion by the azygos nerve. As far as I have observed, only one fibre passes straight through this ganglion, namely, the fibre (*N*) which springs from the bipolar ganglion-cell already described (fig. 2, N) in the lobster embryo, and which is also frequently stained in Astacus. All other fibres appear either to break up in the neuropile of the ganglion, or to be derived from the ganglion cells.

Three pairs of lateral nerves spring from the gastric ganglion. These are represented in fig. 2. The same figure shows several fibres starting from ganglion-cells and entering these nerves. In the adult Astacus the processes of the cells of the gastric ganglion are remarkable for the extraordinary richness of the arborescence of the branches which they give off to the neuropile. Figs. 6 and 7 represent two such cells with their processes. The cell of fig. 6 gives rise to one main fibre, which passes backwards to the bifurcation on the dorsal surface of the stomach. The figure, which is a camera drawing rendered as accurately as possible in all its details, illustrates not only the remarkable richness of the arborescence, but also the characteristic forms in which the finer branches terminate.

Fig. 7 represents a cell from which two main fibres originate.

Looking at the stomatogastric system as a whole, it is probable that there are three main centres from which motor

fibres start and in which sensory fibres end, namely, the two commissural ganglia and the gastric ganglion. The two commissural ganglia are in communication with the central nervous system by means of fibres which enter it from the commissures, and have also a special direct communication with the brain by means of fibres which pass through the anterior median nerve, and bifurcate in the œsophageal ganglion (figs. 1, 3, H). The gastric ganglion is placed in common communication with both commissural ganglia by means of elements originating in cells in the œsophageal ganglion, the processes of which divide into three main branches (*D*). It is also placed in independent communication with each commissural ganglion by means of elements originating in cells of the latter, and running through the œsophageal ganglion.

III.

I propose to add here a few remarks upon the varicose or beaded appearance so often presented by nerve-fibres in preparations made by the methylene blue method, or by the method of Golgi, and on the swellings which occur on the finer nerve-endings. These contain the conclusions arrived at from observations on the adult Astacus, on embryonic lobsters, and on the larvæ of Palæmon and Palæmonetes.

In the two œsophageal commissures of Astacus in fig. 1, I have inserted numerous typical beaded fibres, which illustrate the great variety of appearances presented. In some cases the beads are almost spherical and are joined together by long, thin threads; in others they are elongated spindles, joined by shorter threads, whilst in yet other cases they form long cylinders with pointed ends, the individual ones hanging together by the points.

Figs. 8, 9, 10, and 11 are drawn on a larger scale from preparations stained with methylene blue and fixed with ammonium picrate.

Fig. 8 represents a fibre in which many of the beads are

almost spherical, and are connected by moderately long threads; whilst in fig. 9 they have the form of elongated spindles, and the threads are shorter. In both cases it will be noticed that the beads vary greatly in size and shape, and that the length of the connecting threads also varies.

Fig. 11 represents a nerve-fibre ending in the commissural ganglion, in which the beading has been carried to a somewhat remarkable extent, out of all proportion to the size of the fibre.

Fig. 10, A, B, C, represents three portions of one fibre, which was stained in an œsophageal commissure of Astacus. Near the brain the fibre is practically cylindrical (first portion of *A*). The undulations become more strongly marked, producing the appearance of elongated spindles lying close together (*B*) as we pass further back; whilst near the commissural ganglion the spindles are joined together by fairly long threads, and the result is a typical beaded fibre (*C*). Thus we have the various stages all represented on a single fibre. Such cases are not uncommon, and they alone make it practically certain that the cylindrical form is the normal condition of the fibre, the beaded condition being due to some external cause. It was observed that when the object was unduly stretched or pulled about in the process of preparation, the number of beaded fibres very largely increased.[1]

My observations on embryonic and larval forms have been

[1] The larger fibres, when stained with methylene blue and preserved in ammonium picrate, generally have the surface covered with deeply stained granules, which are either arranged irregularly, as in figs. 8—11, or may lie in longitudinal rows, as in fig. 7. It is not possible to say, in my opinion, whether these are entirely artificial, or whether they may be taken as an indication of the structure of the protoplasm composing the fibre. The latter view has been held by Dogiel ('Arch. mikr. Anat.,' 41, 1893), who appears to consider the fibrillar structure as demonstrated. I should like to draw the attention of those interested in this question to the large black chromatophore masses of Mysis flexuosa. When these are expanded, the pigmented protoplasm in the larger processes is arranged in parallel strands. After soaking for some time in sea water, these strands break up into short pieces and give rise to an appearance which resembles very closely that represented on the nerve-fibre in fig. 7.

even more conclusive in showing that the cylindrical form is the normal condition of the fibre. In the lobster embryos, where I have been able to identify a good many different elements, it has been observed that the same fibre, although generally cylindrical, may at times appear beaded, and that a particular fibre may be cylindrical when it first stains, but afterwards become beaded. This latter fact, which can be readily observed, places the question beyond doubt. That the result, however, can be produced by mechanical means, and is not always entirely due to the reagent, is shown by the following observation. In the lobster embryo there is a single pair of fibres running along the whole length of the cord, the so-called giant fibres, which have a diameter very much greater than any other fibres of the cord. These can be seen quite clearly in fresh embryos, before staining has taken place, and are generally cylindrical. In an embryo, however, which has been roughly handled in the preparation, I have observed that these fibres, whilst still unstained, are distinctly beaded.

The rapidity with which a fibre beads appears to depend to a large extent upon its absolute diameter, and this point is of great importance in selecting suitable objects upon which to study the histology of the nervous system. The fine branches are always the first to assume the varicose condition, and in them the process of beading is carried to such an extent that the fibre breaks up entirely into drops, which do not even hold together. For this reason it is often difficult to obtain staining of the whole of an element in the lobster embryo at the same time, the finer branches being completely broken up into drops before the cell has commenced to stain. The finer longitudinal fibres also become beaded much more quickly and more frequently than the coarser ones.

In the larvæ of the smaller Decapods, as for example Palæmon, Palæmonetes, &c., where the fibres are all very fine, it becomes impossible to obtain useful preparations on account of the rapidity with which the beading takes place. The whole of the neuropile rapidly becomes converted into a mass of small blue drops, which appear to have lost all continuity. Hence

in selecting suitable objects for study, those animals in which the nerve-fibres are coarsest will be most likely to give good results.

Ramon[1] has also noticed, in studying the retina of Vertebrates, that the more delicate the structure, the more difficult it becomes to obtain satisfactory impregnation by Golgi's method. This tendency on the part of fine nerve-fibres to break up into drops appears to me to explain, to a large extent, the impossibility of satisfactorily making out any structure in the neuropile (punkt-substance) when preserved by ordinary methods.

Another phenomenon, which at first sight closely resembles the beading of nerve-fibres, is the formation of small swellings on the terminal branches of a nerve-ending. These have been often described, and for a number of typical instances I may refer to fig. 6, and the finer branches of fig. 11. It will be seen that these swellings usually occur at the angles, where fine twigs are given off, and it is not unlikely that this is always the case, though in some instances the branch has not stained.

From the facts recorded above concerning the beading of fibres, especially the direct observation that the finer branches do assume the varicose appearance much more rapidly than any others, I should have been led to consider it probable that these end-swellings were post-mortem products, and were found in that particular position so constantly on account of the fineness of the fibres. In examining living lobster embryos, however, I was struck with the appearance presented by the terminal branches of the bright red pigment cells or chromatophores, which occur in large numbers. Fig. 12 (a) represents such a chromatophore, whilst fig. 12 (b), (c), (d), (e), and (f) shows individual terminal branches of other cells. Such appearances can be observed in favorable cases even before the embryo is removed from the egg membranes, and when there cannot be the slightest doubt that the animal is alive

[1] Ramon y Cajal, 'La Cellule,' ix, 1893 (quoted in 'Journ. Micr. Soc.,' pt. 5, 1893).

and in its normal condition. It will be seen that the terminal swellings are of exactly the same nature as those found on the nerve-endings. (Compare figs. 6 and 12.) Hence this is clearly a form which fine branches of living protoplasm are capable of assuming. Under these circumstances, in the absence of direct observation to the contrary, it seems more natural to suppose that the terminal swellings on the nerve-endings also represent the normal condition.

In this connection the recent observations of Ballowitz[1] upon the chromatophores of fishes are of interest, confirming the fact that the retractile pigmented protoplasm represents only a portion of the protoplasm of the cell process, the process itself remaining always fully expanded. Should this view be correct, the question naturally arises, does the portion of a branching nerve-fibre which takes up methylene blue represent the whole protoplasm, or only that portion which corresponds to the pigmented protoplasm of the chromatophore?

Both the phenomena of beading and the formation of end-swellings appear to be due to a simple physical cause, namely the difference of surface tension between two fluids. A fluid cylinder surrounded by some other fluid of different surface tension is in a condition of unstable equilibrium, and tends to break up into spherical drops. A stream of water issuing through a circular orifice and allowed to fall for some distance, goes through much the same series of changes as those which have been described for a beaded nerve-fibre, until it finally breaks up into spherical drops. I have been able to produce fibres which have almost exactly the same size and assume the same variety of shapes as beaded nerve-fibres in a very simple way. A thick syrup of gum and sugar is made, and a drop of this is placed in the centre of a glass slide, which has been covered with a layer of paraffin oil. If fine threads are drawn from the syrup across the oiled surface of the glass, with the point of a knife or a rough needle, on examining under the

[1] Ballowitz, "Die Nervenendigungen der Pigmentzellen," 'Zeitschr. wiss. Zool.,' 56, 1893; "Ueber die Bewegungserscheinungen der Pigmentzellen," 'Biol. Centr. bl.,' xiii, 1893, p. 625.

microscope these threads will be seen to be beaded, and generally show all the various forms assumed by nerve-fibres.

EXPLANATION OF PLATES 37 and 38,

Illustrating Mr. Edgar J. Allen's paper on "Studies on the Nervous System of Crustacea."

Fig. 1.—Diagrammatic view of the connections of the stomatogastric system of Astacus with the central nervous system. *Br.* Brain. *com.* Œsophageal commissure. *com. gang.* Commissural ganglion. *tr. br.* Transverse bridge behind œsophagus. *œs. gang.* Œsophageal ganglion. *azy.* Azygos nerve. *ant. med. n.* Anterior median nerve. *dors. n.* Dorsal nerve. *vent. n.* Ventral nerve. *a* and *b.* Branches of ventral nerve. *c.* Median nerve from œsophageal ganglion. *d* and *e.* Branches of ventral nerve. *neu.* Neuropile. C_1, C_2. Bipolar ganglion cells. *D.* Unipolar ditto. *H.* Fibre connecting brain with commissural ganglia. *K.* Motor nerve-ending. *J* and *L.* Sensory nerve-cells. *N.* Fibre connecting gastric ganglion with commissural ganglia. *O.* Fibre connecting commissural ganglia.

Fig. 2.—Ditto, of lobster embryo. Lettering same as Fig. 1. *A* and *B.* Cells of commissural ganglia. *F.* Cell of œsophageal ganglion. *gast. gang.* Gastric ganglion. *m. n.* Nerve from commissural ganglion to region round mouth.

Fig. 3.—Œsophageal ganglion of Astacus. Drawn from one preparation. Lettering as in Fig. 1.

Fig. 4.—Lower portion of œsophageal ganglion of Astacus, enlarged. Drawn from one preparation. As in Fig. 1.

Fig. 5.—Ganglion cell from gastric ganglion of adult Astacus, showing connective-tissue sheath with its nuclei. *N.* Nucleus of cell. *n.* Nuclei of sheath. Cell process stained with methylene blue; cell itself only slightly stained. × 420.

Fig. 6.—Ganglion cell of gastric ganglion of adult Astacus, showing branches to neuropile. Methylene blue, fixed with ammonium picrate. Camera drawing. × 250.

Fig. 7.—Ditto, showing two main fibres (I and II). Methylene blue, fixed with ammonium picrate. Camera drawing. × 250.

Figs. 8 and 9.—Beaded nerve-fibres of Astacus. Methylene blue and ammonium picrate. × 420.

Fig. 10.—Three portions of one fibre from commissure of Astacus. Same mode of preparation. × 420.

Fig. 11.—Nerve-ending in commissural ganglion of adult Astacus. Methylene blue and ammonium picrate. × 420.

Fig. 12.—(a). Chromatophore of lobster embryo. (b), (c), (d), (e), (f). Endings of branches of chromatophores from lobster embryo, showing end-swellings.

The Sensory Canal System of Fishes.

Part I.—Ganoidei.

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With Plates 39 and 40.

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i. Introductory.

I have been led to take up these investigations upon the sensory canal system of fishes at the suggestion of Professor Bridge, to whom I am deeply indebted for the very generous manner in which he has placed at my disposal specimens of very many valuable Ganoids and Teleosts, and for his valuable criticism, assistance, and advice.

The importance of the sensory canal system in fishes has not yet been sufficiently estimated, partly, I believe, from the absence of any continued and systematic investigations concerning the same, and the need of more detailed and reliable information upon the development and early stages. The present series of papers will endeavour in some measure to meet the first requirement, and may in a few instances add to our knowledge of the ontogeny.

It seems strange, considering the important modifications that the skull and cranial nerves have undergone, due very largely to the presence of a sensory canal system, and also the bearing it has upon the origin of various sensory organs, that it has not hitherto been subjected to a more prolonged and thorough examination. So far as I can gather from the voluminous literature upon the subject, previous writers, with one or two exceptions, have been content to simply describe the course of the canals and their branches, omitting any account of the innervation or histology, whilst comparisons with other species, orders, &c., are almost unknown.

In pursuing these inquiries I have placed myself under many obligations to Professor T. W. Bridge, M.A., of Mason College, Birmingham, for his very generous and continued assistance and advice; to Dr. Günther, F.R.S., of the British Museum, London, for the facilities which he has at all times given me for examining the collections under his care. I take this opportunity of expressing my thanks to the Council of the Birmingham Philosophical Society for a grant from their 'Research Fund' in aid of these investigations, and to Professor G. B. Howes, Professor J. Cosar Ewart, F.R.S., and Mr. Samuel Garman for assistance or advice they have from time to time so willingly rendered.

ii. Historical.

The earliest reference to the system of organs known as "muciparous canals," "sense-organs of the lateral line," "branchial sense-organs," "lateral canals," &c., is the description by Stenonis (78) in 1664 of the mucous canals in a

species of skate, and in 1669 of a similar system in one of the sharks. Lorenzini (50) in 1678 confirmed the observations of Stenonis and separated the canals into two systems, viz. sensory and ampullary canals. Monro secundus (56) in 1785 investigated and figured the canals in the head of a cod and a skate; he further traced the innervation of the ampullary canals. Seeing that Monro regarded the system as one for the secretion of mucus, it seems probable that he was not acquainted with Lorenzini's work. Geoffrey St. Hilaire (34), 1802, regarded the mucous ducts as the analogues of the electric organs of the torpedo. Jacobson (38), 1813, was the first to put forward a theory that this system of canals were sensory organs for the transmission of vibrations of the water to the nerves. His theory was more or less supported by Treviranus, Knox, and others. Mayer, 1843, Jobert de Lamballe (40), 1858, and M'Donnell (51), 1861, all regarded them as electric organs; while Blainville, 1822, Savi, 1840, and Robin (64) held that they were mucous canals.

Wagner, 1847, H. Müller, 1851, Kölliker, 1856–8, Max Schultz, 1862, Boll (10), 1868, and many other anatomists gave considerable attention to the subject, but little advance was made until 1868, when Leydig (48) published his comprehensive paper. Commencing in 1850, his series of papers form by far the most complete and important contribution to the subject that has yet been published.

More recent contributions on the development, innervation, and histology have been advanced by Götte, Semper, Balfour (3 and 4), Solger (72, &c.), Eisig (23), Dercum (21), van Wijhe (82 and 83), Hoffmann (35), Wright (84), Fritsch (28 and 29), Sappey (67), Beard (7), and others.

De Sede (22) in 1884 published an interesting paper detailing his results upon the function. He was the first to compare the system with a view to ascertaining its value in classification, and in the Selachia accords to them greater importance for such purposes than in the Teleostei. Garman (32) in 1888, in an exceedingly valuable paper, described and figured the course of the canals in a large series of Selachia and Holo-

cephali, with a view to ascertaining, like de Sede, their value in classification. For this system of canals, &c., Garman proposed the term Tremognosters, but it has not met with general acceptance, the term sensory canal being much more appropriate.

Allis (1) in 1889 dealt in an able manner with the topography and development of the system in Amia calva. Pollard (62) in 1892, following Garman, compared the canals in a number of Siluroids and discussed their value for purposes of classification.

In 1892 Ewart (25 and 26), following up his researches upon the cranial nerves of Elasmobranchs, published a valuable account of the system in Læmargus and Raia batis, the first that has attempted with any completeness to deal with the general anatomy of the system in the Elasmobranchii. He emphasised the necessity for studying this system of sensory canals and their innervation together. He has shown that the canals in the Elasmobranchii, instead of being innervated by the branches of the trigeminal and facial nerves—as was generally supposed—are supplied by the latter only and the vagus. He further pointed out that certain branches of particular cranial nerves are developed solely for the innervation of, and in connection with, the sensory canals, and disappear almost, if not entirely, in the higher Vertebrates.

In 1893 the writer published short accounts of the system in Polypterus, Calamoichthys (18), and Lepidosteus (19), and in certain fossil fishes (20).

For many of the earlier historical details I am indebted to Mr. S. Garman, C.M.Z.S., of the Museum of Comparative Zoology, Cambridge, U.S.A., to whose memoir the reader is referred for more detailed accounts of the opinions of the various writers.

iii. Nomenclature.

It will be as well at the outset of these investigations to revise the nomenclature of the subject, and so avoid an endless confusion and series of explanations which otherwise must

necessarily ensue. And here let me remark in passing that the system adopted by some authors—particularly Garman (32) and Allis (1)—of naming every separate branch a canal is one which I cannot assent to, for even were there a separate source of innervation to each and all of these branches, it is very questionable whether any purpose is served by adding a burdensome nomenclature; and further, when we come to review the sensory canal system in fishes generally, we find that the conclusions arrived at do not support such a method.

In the most generalised forms the canals are simple open grooves, or grooves covered by scales, e. g. Heptanchus. There are a few exceptions to this in the deep-sea Teleosts such as Cottus bathybius, Liparis micropus, Lycodes muræna, &c. The gradual specialisation to dermal canals, then canals partly dermal and partly borne by short drainpipe-like canal bones, then bony channels, and finally passing through the cranial and other bones, is readily traced in the Ganoids and Physostomous Teleosts.

From what little we know of the development of these canals, the gradual evolution of the system is further borne out, for we find that they make their appearance first as isolated grooves, which coalesce and form canals, and these again join with others to form a network more or less distributed over the head.

The whole question of the origin and evolution of this system I hope to discuss in some detail in a later paper. For the present, therefore, I think it advisable to treat the whole series of sensory organs, canals, pits, pores, &c., as one system, and to divide what have been termed canals into a series of branches. We must not lose sight of the fact that, whatever their origin or function, this system is of great importance to the fish, and is consequently subject to endless modifications, and therefore, in the present state of our knowledge, it would, I think, be unwise to lay down any hard-and-fast rule respecting this subject of nomenclature. The scheme I have tabulated below, I think most morphologists will agree, is one based on broad and general principles, and will greatly facili-

tate future investigations, obviating complications and misunderstandings that are sure to ensue from a disregard of some such system.

1. The system of canals, branches, sense-organs, &c., I shall term the sensory canal system.

2. The canal passing from the tail along the lateral portions of the trunk will be spoken of as the lateral canal—the term main canal is used in referring to the anterior portion of the lateral canal traversing the head. The various branches from the main canal which traverse the region of the head will be referred to respectively as the supra-orbital, the sub-orbital, and the opercula-mandibular or hyomandibular branches; and the supra-occipital, the pre-orbital, and the ethmoidal commissures. Where a dorsal canal is present on the body it is spoken of as such.

3. A system of fine dermal canals running from the main canal or a branch of the same, and opening by a series of fine branches to the surface by isolated pores, will be termed cluster pores (= peripheral organs of Allis).

4. The fine pore-like openings spoken of as "pin-hole" pores by many authors I shall term primitive pores, as illustrating the most generalised form, e. g. certain Elasmobranchs and Polyodon, Psepherus, and Acipenser.

5. Those canals which are unbranched and radiate from a given number of centres in the region of the head, having an expanded proximal end or ampulla, and opening to the surface by their distal end, and often spoken of as the canals of Lorenzini, I shall—following Ewart—refer to as ampullary canals.

6. The series of organs known as smell-buds, sense-organs, pit-organs, Merkel's buds, branchial sense-organs, &c., will be termed sensory organs.

iv. Function.

Of the function of this system but little is known. Lorenzini (50), 1678, was probably the first to regard it as a sensory one. Jacobson (38), 1813, stated its function more definitely; but,

as has been previously pointed out, until the publication of Leydig's papers most authors either regarded its function as an electric one or as a system of canals simply for the secretion of mucus.

Leydig drew attention to the relations of the system with the auditory organ, and compared the canals, &c., with the ampullæ; later, however, he suggested that the system was one of some unknown function, which he termed a sixth sense.

The most probable theory is that advanced by Schulze (69) in 1861, viz. that this system of canals, &c., is one for the perception of wave vibrations and oscillations; to which it were as well, perhaps, to add Krause's theory, 1875, that they also serve to give notice of chemical or physical changes in the water.

Dercum (21), 1879; Emory (24), 1880; and Bodenstein (9), 1882, have each pointed out relations to the auditory organ.

Beard (7), 1886, in a brilliant paper, showed that the organs of this system have some physiological relationship with the gill-clefts, and that the auditory and olfactory organs are but specialised sense-organs of the sensory canal system.

Ayers (2), 1892, in a voluminous and highly speculative treatise, has also pointed out the relations of the auditory organ to the sense-organs of this canal system; and although this author sums up many such weighty questions in Vertebrate morphology upon very little evidence and in a somewhat hasty manner, he has nevertheless brought forward a number of points which greatly tend to strengthen Beard's theory,—one of the most important, perhaps, being his discovery that "in Elasmobranchs the structural connection between the ear organs and the surface canal organs is for a long time maintained after the ear has migrated to its internal home, and in some forms may be said with truth to persist during the life of the individual" (p. 315).

A number of authors—Eisig (23), Whitman, Leydig—have pointed out the relations of the segmental sense-organs of Invertebrates to those of Vertebrates. Some of these I shall have occasion to discuss in a later paper.

v. The Cranial and other Bones.

A brief description of the cranial and other bones of the head will facilitate reference to the course and distribution of the sensory canal system.

The nomenclature is mainly that used by Bridge (16).

Post-temporals (Pl. 39, fig. 1, *pt.*) are two somewhat Y-shaped lateral splints, the innermost area being much the shorter. Upon the surface of these elements are a series of canal bones, which conduct the posterior portion of the main canal.

Dermo-sphenotics (Pl. 39, fig. 1, *d. sph.*).—The dermo-sphenotics are almost hidden by the development upon their surface of a series of much expanded canal bones. Posteriorly the dermo-sphenotics are bounded by the post-temporals, anteriorly by the dermo-ect-ethmoids. On their inner side they are produced into a lateral process, the sutural margin of which is closely interwoven with the parietal and frontal sutures.

Over the dermo-sphenotics the main canal divides into the supra- and sub-orbital and hyomandibular branches.

The dermo-ect-ethmoids (Pl. 39, fig. 1, *d. ec. eth.*) are two lateral parostoses lying over the olfactory region and forming the lateral boundaries of the frontals.

The parietals (Pl. 39, fig. 1, *pa.*) are two elongated splints on either side of the median line. They do not oppose each other mesially, excepting in the most posterior portion, at least not in the specimens I have seen. Bridge (16), however, says they do, and figures them so, from which it would appear that there is a considerable amount of variation. Anteriorly they dovetail with the frontals, posteriorly terminating in a number of fibrous-like rays. The parietals extend from the occipital region to just behind the orbit. They are the largest and the thickest of the cranial splints.

The frontals (Pl. 39, fig. 1, *fr.*) lie on either side of the dermo-ethmoid, extending forwards for some distance. They

are two irregular and unequal splints, and, like the parietals, do not meet in the median line.

The dermo-ethmoid (Pl. 39, fig. 1, *d. eth.*) lies between the anterior portion of the frontals. Anteriorly it terminates in a long pointed process.

The circumorbital series are the canal bones which conduct the suborbital branch of the main canal of the head—after passing over the dermo-sphenotic—along the posterior and inferior borders of the orbit. They are a series of tube-like bones and pass beneath the dermo-ect-ethmoid.

The parasphenoid extends from the occipital region to a point slightly anterior to the nasal capsules. Its anterior portion is invested by two median splints—the vomers.

The hyomandibular is a slender shaft-like bone. Its proximal end fits in a groove on the lateral border of the otic capsule. Its distal end is attached to the symplectic cartilage. The axis of the hyomandibular "is inclined backwards at an angle of less than 30° with the cranio-spinal cartilage."

The maxilla is a thin splint-like bone closely adherent in the anterior portion to the scale-like mesopterygoid and the surrounding cartilage; the middle portion is separated from the pterygoid process by the levator mandibularis muscle, whilst the posterior portion adheres to the obitar process of the pterygoid bar.

The branch of the sensory canal passing along the maxilla is a dermal one, and does not enter into the substance of the bone at all.

The mandible consists of a long dentary splint closely applied to the Meckelian cartilage. There is no angular element or os articulare.

The mandibular branch of the sensory canal, like the maxillary, is a dermal one, and passes over the surface of the splint.

vi. Polyodon folium.

So far as I am aware there is no reference in any of the accounts of the anatomy of Polyodon to the sensory canal system, excepting a passing notice by van Wijhe (82).

In P. folium there are present all the canals and sensory organs previously referred to, excepting the ampullary canals, which have not as yet been observed in any order of fishes but the Elasmobranchii.

The system extends from the dorsally deflected terminal portion of the trunk, which I shall speak of as the dorsal caudal fin, to the tip of the rostrum. There is a certain polarity about the system, it having its greatest development on the head and rostrum, and the posterior end of the trunk of the body and the dorsal caudal fin. Short branches of the lateral canal cover each side of the body, terminating in series of cluster pores.

The general distribution of the canals and branches is as follows:

The lateral canal commences about 180 mm. from the tip of the dorsal caudal fin and passes along the side of the body, giving off in its course the above-mentioned branches, which are mostly ventral ones. The cluster pores on these branches exhibit slight modifications from those upon the head. The canal at the anterior end of the body makes an upward curve and enters upon the skull in the post-temporal region as a dermal canal. Traversing the region for a short distance, it enters a canal bone and gives off a small branch on the inner side of the canal in the occipital region. The canal is continued forwards in a series of canal bones lying on the dorsal surface of the dermo-sphenotic of Bridge, giving off a short lateral branch at the most posterior end of the bone. In the anterior portion the canal bone spreads out in a wing-like manner and divides into two dorsal branches, viz. a supra- and sub-orbital, and a ventral branch, the hyomandibular (Pl. 39, fig. 1). The first-mentioned branch passes upwards and forwards, skirting the lateral border of the frontal; it then takes a downward course along the dermo-ect-ethmoid and passes between the nasal openings, below which it unites with the sub-orbital branch. The sub-orbital branch is given off in the anterior portion of the dermo-sphenotic, and runs as a bony canal posterior and inferior to the orbit, meeting anteriorly

with the supra-orbital branch,—thus bringing about a condition not at present known to occur in any other investigated fish.

Following the coalescence of these two branches on the ventral surface of the rostrum, the course now lies forwards and inwards, the canal being conducted by a series of canal bones, to which reference will be made later. It continues forwards, diverging laterally in the anterior portion, and meets with its fellow of the opposite side.

Traversing the lateral and posterior portion of the parietals are two small branches passing from the main canal towards the median line, but which, however, do not form a commissure. The hyomandibular branch, as previously pointed out, passes off from the posterior lateral border of the dermosphenotic. It is continued as a dermal canal to the angle of the mouth, where it divides into two finer branches, the dorsal one passing along part of the maxilla, and the ventral one along the mandible. A series of small branches pass off from the hyomandibular portion and are distributed over the opercular-flap, and terminate in cluster and primitive pores (Pl. 39, fig. 3, *c. p.* and *p. p.*).

It will be seen from the preceding account that the system, in so far as the canals and branches are concerned, is one of a very simple character.

We will now examine the various branches, pores, &c., in detail.

1. The Lateral Canal.—Commencing about 180 mm. from the tip of the dorsal caudal fin as a fine dermal canal giving off numerous branches, the lateral canal passes forwards and downwards, and then dorsally again after this slight ventral flexure. It continues along the dorso-lateral border of the body, becoming dorsal previous to entering upon the head. During its course from the caudal to the cranial region there is a gradual, but distinctly appreciable, enlargement in its diameter.

There are from thirty-two to thirty-five branches given off during the whole length of the canal, of which twelve are

dorsal and twenty-two ventral, fourteen of the twenty-two being situated on the dorsal caudal fin. The number and position may vary on either side of the body. None of the branches are of any great length, ranging from 12 to 17 mm. Each branch terminates in from four to seven still smaller branches opening to the surface by a series of pores (Pl. 39, fig. 2, *l. c. b.*). There are seldom less than two and rarely more than twelve in number. These are the cluster pores.

Along the whole length of the canal and its branches are two series of sensory organs, about which, from the condition my specimens were in for histological purposes, I can say but little. The first are a series, sixteen to twenty in number, of fairly large circular markings—3½ to 4 mm. across—slightly raised above the epidermis. They are distributed at irregular intervals along the canal and open to the surface by a transverse aperture or slit. Sections cut by a freezing microtome showed them to consist of a layer of epithelial cells, with numerous goblet cells forming a follicular-shaped organ. At the base of the follicle a sensory organ was present, in which no difference could be seen from those found in the cluster and primitive pores, excepting in size. From their structure and position I regard them as modified cluster pores and synonymous with the sensory follicles which Fritsch (29) speaks of as "spaltpapillen." Externally they are very like the "seitenorgane" figured by Leydig (49, Taf. viii, fig. 13, *b.*) in Petromyzon.

The second series are much more numerous. They are distributed over the canal and its branches, and also in the immediate neighbourhood. They are present in the greatest number at the posterior end of the body. There are from 800 to 1000 on each side of the body. They are very small, the largest not measuring more than 3 mm. across. They appear as a small ring enclosing a depression in the centre of which arises a small, hard, conical body, opening at the apex by a minute slit-like pore. In one or two cases they were observed in groups (Pl. 39, fig. 6, *b* and *c*); these were not on the canal, but in close proximity. Those upon either the canal or its

branches were always in the form of single papillæ. In the dead Polyodon which had been in alcohol for some years, the apex of the papilla was hard and glossy as if for protection.

2. THE MAIN CANAL OF THE HEAD.—The main canal is a direct dermal continuation of the lateral canal. On the lateral border of the post-temporal region it passes on to the head as a dermal canal, being continued in a canal bone. It passes forwards along the dermo-sphenotic, on which bone it gives off a short lateral branch which terminates in a cluster pore. Wing-like processes extend over the anterior portion of the dermo-sphenotic, by which the canal is divided into three branches—the supra- and sub-orbital, both dorsal, and a posterior ventral one, the hyomandibular.

The Supra-orbital Branch.—Leaving the main canal on the inner border of the anterior portion of the dermo-sphenotic, it passes forwards over the posterior lateral border of the frontal, giving off in its course three small branches (Pl. 39, fig. 1) which continue as dermal canals for a short distance, and then each divides into still smaller branches, all of which open to the surface by a series of cluster pores. From the frontal bone the branch then takes a downward course, across the dermo-ect-ethmoid suture, between the nasal openings, and joins the sub-orbital branch.

The Sub-orbital Branch.—The sub-orbital branch passes off from the main canal on the outer border of the anterior portion of the dermo-sphenotic, and is conducted around the posterior and inferior borders of the orbit in a series of small canal bones. On the ventral surface beneath the dermo-ect-ethmoid it joins with the supra-orbital branch, and the two are conducted as one canal in a series of canal bones which pass forwards and inwards towards the parasphenoid and continue along its ventral and lateral border. In their course forwards two lateral branches pass off, and break up in a series of very minute dendriform branches.

Approaching the anterior portion of the rostrum the diameter of the canal becomes less, diverges laterally, and passes

around the anterior border, joining with its fellow half of the opposite side in the median line (Pl. 39, fig. 11).

The Hyomandibular Branch.—Leaving the main canal slightly posterior to the division resulting in the supra- and sub-orbital branches, the hyomandibular branch passes backwards as a dermal branch over the region of the hyomandibular bone to the angle of the mouth, where it divides into two smaller branches of much less diameter, viz. a mandibular and a maxillary branch; the former is the larger, and passes along the mandible, the latter traversing the upper jaw for a short distance. Neither meet with the companion branches of the opposite side. In the course of the hyomandibular branch from the dermo-sphenotic to the angle of the mouth there are twelve branches given off. They are similar in all appearances to those previously described on the lateral canal, only here there are dense patches of primitive pores also, in close connection with the terminations of the branches (Pl. 39, fig. 3). The branch *a* shows both cluster and primitive pores at the terminations of the smaller branches. Judging from the two examples I have investigated of Polyodon, I should say that it is a feature of rare occurrence for a branch to terminate in primitive pores only, as in Pl. 39, fig. 3, *b*.

3. The Commissures.—There are no true commissures present in the sensory canal system of Polyodon. In the numerous fishes in which this system has been investigated, the Polyodontidæ are the only family in which as yet the commissures are known to be absent.

On either side of the occipital series of canal bones branches from the main canal pass inwards, as if to meet in the median line, but, leaving their bony channel, they divide into three series of cluster pores, those of the one side having no connection with their companions of the opposite side (Pl. 39, fig. 1).

A similar condition is found in the region of the pre-orbital commissure. From the supra-orbital branch three smaller branches pass off as short bony channels, and are continued for a short distance as dermal canals, each terminating in a series

of cluster pores. There is no connection between the two sides (Pl. 39, fig. 1).

4. THE CLUSTER PORES.—Distributed over the head and along the sides of the body are a series of organs which I have termed cluster pores. They are subject to great variation in both number, location, and form—a fact which seems to have been lost sight of by many observers.

On a specimen of Polyodon, 1660 mm. in length, there were counted 132 series or patches of these pores, distributed as follows:

On each side of the head . .	12	=	24
On the dorsal surface of the head .	38	=	38
On each side of the body . .	35	=	70
			132

Each series of pores arises as a small single branch from the lateral or main canal, or one of its chief branches; it traverses the surface for a short distance and then divides into from three to twelve still smaller branches, each of which opens to the surface by a small oval or circular pore, the peripheral border of which is pigmented. In a few cases division of the terminal branches was noted, the pores assuming the form of the figure 8. Fig. 6 *d* (Pl. 39) illustrates one taken from the lateral canal.

In longitudinal and transverse sections the following structure was noted. They agree almost in every detail with the "spalt-papillen" of Fritsch. The neck is surrounded by a layer of epithelial cells, at the base of which a series of columnar supporting cells—whose nuclei stain deeply—surround a series of pyriform sense-cells containing large oval nuclei at their inner and lower ends and hair-like processes at the opposite ends. The supporting cells are surrounded by the epidermis. At the base of the layers of columnar epithelium nerve branches pass, which break up into a series of fine terminal fibres and pass into the sense-cells (Pl. 39, fig. 4).

5. THE PRIMITIVE PORES.—These are strictly confined to the region of the head and rostrum. In Polyodon they are developed to an enormous extent, covering the whole of the

head, rostrum, and gill-flaps in the greatest profusion (Pl. 39, fig. 5).

On the specimen in which the cluster-pores were counted there were about 3500 groups of primitive pores, the number of pores in each group varying from seven to seventeen.

The diameter of a pore was almost equal to the distance from the surface to the sensory organ lying at its base.

Histologically they appeared to be miniature cluster-pores. It has been very generally supposed that the sensory organs of the lateral canal differed from those in the canals of the head. Excepting in size I have been unable to distinguish any differences worthy of note in those in Polyodon and Acipenser. Ewart (26) states that this difference does not exist, and in Raia finds that "parts of the cranial canals exactly agree in structure with the canals of the trunk" (p. 98).

So far as I have been able to ascertain, these primitive pores are found only in the Selacheoid Ganoids in the form I have figured on Pl. 39, figs. 2 and 3, *p.p.*, viz. in series aggregated into distinct pigmented patches.

vii. Innervation of the Canals.

The cranial nervous system of Polyodon exhibits a number of interesting features at present not known to occur in any other Ganoid.

From the large number of sensory organs I expected to find great branching of the facial nerve and possibly the trigeminal also, and generally a condition not unlike that figured by Ewart in Læmargus (25). Indeed, I have endeavoured to interpret the cranial nerves in the light of this author's recent researches, which have placed the study of the cranial neurology of fishes and Vertebrates generally in quite a new aspect.

In Polyodon there are three features which have greatly modified the number and distribution of the cranial nerves, viz.:

(i) The unusual number of sensory organs;

(ii) The backward position of the suspensorium (hyomandibular); and

(iii) The largely developed rostrum.

The principal nerve groups innervating the sensory canal system are the trigeminal, the facial, and the vagus. The fact of the trigeminal actually innervating a part of the sensory canal system is of special interest, seeing that Ewart (25) found that in Læmargus and Raia the innervation proceeded from the facial and vagus only.[1]

The cranial nerves of Polyodon have been briefly described by van Wijhe in his memoir on the cranial nerves of Ganoids[2] (82). For purposes of comparison I have reproduced his figure, and it will at once be seen that there are a number of important differences between his description and figure and those here given (Pl. 40, figs. 9 and 10).

Van Wijhe (82, p. 240) states that the specimen he worked at was a young one and only small. It is probably owing to the fineness of the nerves in such a specimen, of which he frequently makes mention, that our accounts differ so widely from one another.

The Trigeminal group may be divided into five branches, viz.—

1. The Ramus opthalmicus superficialis.
2. The Ramus opthalmicus profundus.
3. The Ramus maxillaris.
4. The Ramus mandibularis.
5. The Ramus oticus.

1. The ramus opthalmicus superficialis is the most anterior branch of the group, and passes forwards dorsal to the orbit and on the inner side of the olfactory capsule.

2. The ramus opthalmicus profundus is given off from the main branch of the trigeminal, and lies ventral to the ramus opthalmicus superficialis and much deeper. In front of the

[1] Ewart treats of the ramus oticus as distinct from the trigeminal nerve.

[2] "Als ich Spatularia untersucht, kannte ich die Wichtigkeit des Verlaufes der Schleimcanäle noch nicht, sodass ich nur sagen kann, dass der mandibulare Zweig vor dem Spritzloche das Cranium verlässt, längs dem Vorderrande des Hyomandibulare und dann zwischen Unterkiefer und Hyoid verläuft. Er liegt unbedeckt in der weissen Haut und fällt sogleich in die Augen; seine Wände sind verknöchert" (p. 247, § 4).

olfactory capsule they run almost parallel to each other. According to van Wijhe it divides into two branches, a dorsal one which passes over the olfactory capsule, and another to the fore part of the orbit.

3. The ramus maxillaris is a large nerve passing beneath the orbit and dorsal to the ramus palatinus of the facial. It passes along the whole length of the rostrum.

4. The ramus mandibularis passes ventral to the hyomandibular bone across the cheek in an oblique direction. Anterior to the symplectic cartilage it divides into two branches, the anterior one sending branches to the muscles and primitive pores in the region of the maxilla, whilst the posterior branch innervates the muscles in the mandibular region.

5. The ramus oticus is the most posterior branch of the trigeminal group. It is a dorsal branch which passes backwards. Van Wijhe describes it as passing dorsally through a canal, and terminating just in front of the foramina of the vagus. In front of the vagus, however, it turns forwards again and innervates the cluster pores between the occipital region and the spiracle (Pl. 40, figs. 11 and 12, *r. ot.*).

The Facial group consists of the following five branches—

1. The Ramus palatinus?
2. The Ramus buccalis.
3. The Ramus mandibularis.
4. The Ramus hyoideus.
5. The Ramus opercularis.

1. The ramus palatinus?—Presumably this is the ramus palatinus of van Wijhe. It is the most anterior branch of the facial, and passes beneath the orbit and olfactory capsule, having an almost parallel course to the ramus buccalis (Pl. 40, fig. 11, *r. p.*).

2. The ramus buccalis is the chief branch innervating the canals and sensory organs. In Polyodon it is developed to an unusual extent. Its course lies ventral to the orbit, immediately in front of which it divides into two branches, these again dividing more anteriorly. These are termed respectively *a*, *b*, *c*, *d*, and *e*.

a. The branch *a* is the most dorsal one (Pl. 40, fig. 11, *a*.), and gives off innumerable fine branches from either side, which pass to the combined supra- and sub-orbital branch of the main canal. In the space of 26 mm. fifty-three branches were counted and traced to the canal. In Læmargus, Ewart (25) states that there are over 1500 twigs given off from the facial nerve to the sensory and ampullary canals. In Polyodon there must be 2000 to 3000. In the anterior portion the branch further divides into smaller branches, which terminate either in primitive pores or the anterior portion of the canal.

b. This is only a small branch passing along the rostrum for a little more than half its length. It supplies the primitive pores on the dorsal region of the rostrum.

c and *d*. These two branches supply the primitive pores on the lateral and ventral portion of the rostrum; most of the branches from *d* pass to the two lateral branches given off from the combined supra- and sub-orbital branch of the sensory canal.

e. There is a small branch passing off from the ramus buccalis posterior to the orbit, labelled *e* (Pl. 40, fig. 12). It innervates the circum-orbital series of primitive pores.

Van Wijhe figures the ramus buccalis as a single branch passing directly forwards beneath the olfactory capsule (Pl. 40, fig. 9, *r.m.s.*).

3. The ramus mandibularis.—Van Wijhe's description and figure do not at all correspond to the condition I have found in Polyodon. He figures a ramus mandibularis passing across the centre of the hyomandibular bone, a condition common to the Teleostei, but not at all correct for this fish. In his figure (Pl. 40, fig. 9) it is at once evident that he has the hyomandibular at a wrong angle. Supposing his figure were otherwise correct, which it is not, it would appear in the position I have shown it in in fig. 10, *h. m.* Matters are further complicated by his figuring the ramus hyoideus as a branch of the ramus mandibularis (fig. 9, *r. h.*). This latter is shown as passing beneath the suspensorio-quadratum ligament, and is described as dividing into an internal and external branch. He speaks of the

former as innervating the ventral portion of the mandibular branch of the sensory canal.

I find that the ramus mandibularis—which is quite distinct from the ramus hyoideus—passes beneath the proximal head of the hyomandibular to the angle of the jaw, where it bifurcates and further divides into smaller branches (Pl. 40, fig. 12, *r. m'.*). It innervates some of the primitive pores of the sides of the head and mouth, but not the mandibular branch of the sensory canal, as described by van Wijhe, which is supplied by the ramus opercularis superficialis No. 4 (Pl. 40, fig. 12, *r. o.* 4).

4. The ramus hyoideus is a large branch passing beneath the hyomandibular around the angle of the jaw and along the cerato- and epi-hyal. It does not branch from the ramus mandibularis, but is the ventral division of the ramus opercularis superficialis (Pl. 40, fig. 12, *r. h.*). It passes from the brain to the angle of the jaw beneath the hyomandibular branch of the sensory canal, and dorsal to the ramus mandibularis.

I regard van Wijhe's ramus hyoideus (Pl. 40, fig. 9, *r. h.*) as homologous with the ramus opercularis superficialis No. 4, (Pl. 40, fig. 10), while I think he has mistaken the true hyoidean branch for what he describes and figures as the ramus mandibularis ext. (Pl. 40, fig. 9, *r. m''.*).

5. The ramus opercularis superficialis arises with the ramus hyoideus. Dorsal to the hyomandibular branch of the main sensory canal it divides into four branches. Nos. 1 and 2 pass backwards and break up into a series of finer branches. The branch, *r. o.* 3, fig. 10, traverses the region between Nos. 1 and 2 and the branch 4. This latter passes dorsally along the whole length of the hyomandibular branch of the main sensory canal, which it innervates, and its cluster of primitive pores. At the angle of the jaw, in the region of the symplectic cartilage, it divides into two branches, which innervate the canals of the upper and lower jaws and the majority of the primitive pores.

The ramus opercularis superficialis would seem to be a special branch of the facial for the innervation of the primi-

tive pores, &c., on the sides of the head and gill-flap in Polyodon.

The Glossopharyngeal.—Ewart has suggested that possibly the most anterior portion of the lateral canal may be innervated by nerve-fibres from the glossopharyngeal nerve previous to its leaving the cranial cavity, but so far he has failed in Læmargus to find any branches which pass to either the sensory or ampullary canals from this nerve. In Polyodon I have met with similar results, the anterior portion of the lateral canal being innervated by the branch *l'*. (Pl. 40, fig. 11) of the vagus. This branch also innervates the cluster pores in the occipital region.

The Vagus.—The lateral division of the vagus supplies the lateral canal and its associated organs. It gives off a number of branches all along its course, which innervate the branches, cluster pores, and other sensory organs situated in the region of the canal.

viii. Psepherus gladius.

The sensory canal system of Psepherus approaches very closely to that described in Polyodon, to which it holds the same relation as Calamoichthys does to Polypterus.

From an external examination of specimens in the British Museum little or no difference could be observed in the form and distribution of the canal and its branches.

I have described in Polyodon a series of sensory organs in the region of the lateral canal which I am inclined to regard as modified cluster pores, and synonymous with the "spalt-papillen" of Fritsch. In Psepherus these are rather larger and more numerous.

A partial dissection of the head of a small specimen was made, in which the dermal portions of the main canal and its branches were all found to agree with the condition present in Polyodon.

In the smallest specimens examined there were no cluster or primitive pores visible on the lateral canal, and no trace of branching. In a specimen about 320 mm. long the branches seemed to be in a very early stage of formation.

ix. The Cranial and other Bones.

But a very brief reference is necessary to the cranial and other bones of Acipenser. The nomenclature used is mainly that of Parker (58).

The post-temporals (Pl. 40, fig. 13, *p. t.*) are two large dermal scutes lying at either side of the head, posterior and lateral to the dermo-occipital. They are bounded in front by the epiotics and conduct the main canal.

Epiotics (Pl. 40, fig. 13, *ep.*).—Two irregular scutes having a lateral position to the dermo-occipitals. They form the lateral posterior border of the parietals and the posterior border of the squamosals. In their anterior portion the occipital commissure passes off from the main canal.

Squamosals (Pl. 40, fig. 13, *sq.*).—Two large scutes forming the lateral borders of the parietals. In their anterior portion the main canal divides into the supra- and sub-orbital.

The dermo-ect-ethmoids (= the prefrontals of many authors; Pl. 40, fig. 12, *d. ec. eth.*) lie in front of the squamosals. Ventrally they are bounded by the first of the circum-orbital series; anteriorly they form the dorsal boundary of the orbit, extending as far as the nasal capsules. The chain of canal bones conducting the sub-orbital branch passes over the posterior portion of either side.

Dermo-occipital (Pl. 40, fig. 13, *d. oc.*).—A median somewhat dagger-shaped scute forming the posterior border of the parietals; the most anterior portion passes between the parietals for some distance and is overlapped by them. It is traversed by the occipital commissure.

The parietals (Pl. 40, fig. 12, *pa.*) are two large median scutes bounded posteriorly by the dermo-occipital and epiotics, laterally by the squamosals, and anteriorly by the frontals and dermo-ethmoid. In very large specimens which I have examined the occipital commissure passes through the posterior portion of the parietals as well as the epiotics and the dermo-occipital scute.

The frontals (Pl. 40, fig. 12, *fr.*) lie at either side of the

dermo-ethmoid. They conduct the supra-orbital branch of the main sensory canal, and are bounded laterally by the dermo-ect-ethmoids.

The Sub-orbital Series (Pl. 40, fig. 13, *s. or.*).—There are only two of the orbital scutes visible externally. The upper forms the posterior border of the orbit, and the lower both posterior and inferior borders. The sub-orbital branch of the sensory canal passes through both and then into the two internal ones lying anterior to the orbit.

There is no pre-opercular scute in Acipenser, or any branch of the main sensory canal corresponding to the operculo-mandibular branch in Lepidosteus, &c. What Parker (58) has termed pre-operculum is in all probability the jugal.

There are no mandibular or maxillary branches of the sensory canal in Acipenser, the primitive pores in the immediate region probably functioning in their place.

x. Acipenser sturio.

References to the sensory canal system of Acipenser are found in the writings of M'Donald (52), van Wijhe (82), and others, but most of these are only in relation to the form or position of the scutes on the lateral portion of the body, conducting the lateral canal.

Van Wijhe seems to have found some difficulty in tracing the canals, &c. His account is as follows :—

"Was das System der Schleimcanäle anbelangt, so sind die Röhre beim Stör ausserordentlich fein, nur mit Mühe kann man sie an einigen Stellen durchschimmern sehen. Um ihren Lauf wahrzunehmen wurden sie mit einer feinen Borste sondirt, und dann der Knochen, der sie umschloss, nach der Aussenseite aufgeschlitzt.

"Der Hauptstamm liegt im Supraclaviculare, lateralen Supratemporale (Occip. externum, Gegenb.; epioticum, Huxley) Squamosum, Frontale, asale Nund in der Scheidewand beider Nasenlöcher derselben Seite.

"Die supratemporale Quercommissur liegt hier, eben so wie bei den andern Fischen in den Supratemporalia, deren sich

beim Stör drei vorfinden, ein paariges, oben genanntes, und ein unpaares medianes (Supraoccipitale).

"Der suborbitale Zweig verlässt den Haupstamm in der Mitte des Squamosums, tritt dann in das (dermo-) Postfrontale und läuft weiter nach vorn durch die beiden Infraorbitalia."

In a foot-note he says:—

"Die Lage der Schleimcanäle ist von hohen Interesse bei der Bestimmung der Deckknochen des Schädels, weil sie in Hinsicht auf diese ziemlich constante Beziehungen zeigt."

Commencing some 13½ mm. from the tip of the dorsal caudal fin the lateral canal traverses a number of isolated scutes, anteriorly becoming more dorsal it enters the skull by traversing the dermal ossifications which connect the pectoral arch. Short branches are here given off which ramify the bone. In the post-temporal an occipital commissure passes off from the main canal, which is continued forwards through the epiotic and squamosal. In the squamosal the canal divides into a supra- and sub-orbital branch, the former continuing through the frontal, and passes outwards and downwards behind and posterior to the anterior nasal opening and then along the rostrum, becoming connected with its fellow half of the opposite side, and also ventrally with the sub-orbital branch. This latter branch passes from the division of the main canal in the squamosal into the pre-frontal, and then through a circum-orbital series which surround the posterior and ventral borders of the orbit, some of which are not visible externally. There are four bones in this series. The canal issues from the most anterior as a dermal canal, and passes into another series of canal bones, which are not unlike in appearance a series of miniature drain-pipes; these conduct the canal to the tip of the rostrum, where it now passes into a tooth-shaped bone, in which it branches in various directions, the main branch joining the supra-orbital branch above.

1. The Lateral Canal.—In Acipenser the lateral canal commences about 13½ mm. from the tip of the dorsal caudal fin, in a series of canal bones. Previous to the commencement

of the canal there are a series of these bones. The canal is conducted along the sides of the body by alternating series of these small bones and of isolated scutes, into which latter the canal enters posteriorly and on the ventral side, passing out anteriorly and on the dorsal side. The number of these small drain-pipe-like bones between each scute varies from four to ten. The greater portion of the canal is exceedingly small in diameter, increasing slightly in the anterior portion.

There are no branches given off from the lateral canal, neither in or on the scutes or from the intervening portions. There is also a complete absence of cluster or primitive pores.

2. The Main Canal of the Head.—The main canal enters the skull by traversing the lateral border of the post-temporal. It is continued forwards through the epiotic, in the anterior portion of which it gives off the occipital commissure. Entering the squamosal the canal passes forwards to a central position and divides into two branches, the supra- and sub-orbital.

The Supra-orbital Branch.—Leaving the main canal in the squamosal, the supra-orbital branch takes an inward and forward direction; passing through the frontal bone, in which it gives off two lateral branches, it takes an outward course between the nasal apertures and is continued on the dorso-lateral border of the rostrum, again passing into a series of drain-pipe-like bones. In the most anterior portion it makes a ventral turn and joins with the sub-orbital branch by passing through a small tooth-shaped bone (Pl. 39, fig. 7, *a* and *b*).

The Sub-orbital Branch.—After separating from the main canal, the sub-orbital branch passes in a lateral direction into the pre-frontal and then through a series of circum-orbital bones, of which there are four, the second forming the posterior ventral angle, while the third and fourth are not visible externally. Leaving these bones as a dermal canal, it enters a series of drain-pipe-like bones by which it is conducted along the ventral and lateral borders of the rostrum. In the anterior portion it makes a slight lateral divergence and passes

around the anterior border of the rostrum, joining with its fellow of the opposite side.

These bones which I have spoken of as drain-pipe-like canal bones are exceedingly interesting in that they probably represent the earliest trace we have of an ossified investment of the sensory canal system.

In Polyodon and Psepherus they are long thin-walled bony channels in the greater portion of the head, none occurring on the lateral canal. They never assume the disc-like form found in Acipenser (Pl. 39, fig. 7, *c*). They average from 3 to 9 mm. in length, some few on the dorsal surface of the head being much larger.

In Acipenser they are present both on the head and in connection with the lateral canal. Those on the head vary in shape and size, some being pipe-like in form, others irregular. The simplest form in which they were found is shown in fig. 7, *c* (Pl. 39). These were taken from the anterior portion of the sub-orbital branch. They are thin disc-like pieces of bone measuring from $4\frac{1}{2}$ to 7 mm. across and about $\frac{1}{4}$ mm. in thickness. Similar forms, only thicker, were found in the same species conducting the lateral canal.

3. The Pores.—In Acipenser there are no structures that can be regarded as cluster-pores. On the ventral surface of the rostrum there are numerous patches or groups of primitive pores which are similar in all respects to those previously described in Polyodon. In a sturgeon measuring 10 feet 3 inches in length upwards of eight hundred of these groups were counted.

xi. Summary and Conclusion.

In summarising the more important features resulting from this investigation, it will already have been observed that perhaps the most important evidence obtained is that bearing upon the Elasmobranch character of Polyodon and of the Selachoid Ganoids generally.

The Selachoid Ganoids are the first group of fishes as yet

known which show the gradual specialisation of a dermal canal to one enclosed in a bony tube and then in bony plates.

The system of pores, sensory organs, &c., is one showing the modifications and evolution of a sense-organ.

The form, number, and branching of the cranial nerves has been very largely modified by the presence of an innumerable series of sensory organs (cluster and primitive pores, &c.) distributed over the cephalic region.

The Ganoids as a group have very rightly been divided by Bridge (16) into Selachoidei and Teleosteoidei. For the retention of the group there seems to be sufficient morphological evidence. Not a few zoologists would join the Ganoids with the Teleosts. Possibly there are forms included in the Ganoids whose affinities are undoubtedly with the Teleosts, but the division termed by Bridge Selachoidei is much more closely allied to the Elasmobranchs. Indeed the position, origin, number, and course of the cranial nerves in Polyodon suggests a much closer relationship to this latter group than even Bridge supposed, who was the first, I believe, to institute a comparison between them.

The conclusions of Ewart (26) are very largely confirmed and augmented by this investigation.

From the variability of the sensory canal system in the Ganoids but little importance can be attached to it for purposes of classification, other than of the most generalised nature.

xii. Comparison of Polyodon with Acipenser.

As we should naturally expect, there is a great difference in the sensory canal system of the two forms. Polyodon, on the one hand, may be regarded as a form on the very border-line between the Elasmobranchii and the Selacheoid group of Ganoids, whilst Acipenser, on the other hand, may be placed on the border-line between the latter group and the Teleosteoid Ganoids.

Although widely separated from one another by very many important differences, the two species show at the same time a

number of features common to both. These may be summarised as follows:

Polyodon differs from Acipenser in—

(*a*) The canals being largely dermal ones, e. g. the lateral canal part of the main canal of the head and its branches—none passing through any of the cranial elements.

(*b*) The presence of branches on the lateral canal and on the hyomandibular branch of the main canal.

(*c*) The absence of commissures.

(*d*) The peculiar course and coalescence of the supra- and sub-orbital branches, by which a single canal is formed which does not pass along the lateral borders of the rostrum, but on either side of the parasphenoid.

(*e*) The presence of small mandibular and maxillary branches, a feature of great interest considering the many Elasmobranch affinities of the fish.

(*f*) The presence of cluster pores and other sensory organs on the lateral canal.

The sensory canal system of Polyodon agrees with that of Acipenser in—

(*a*) The presence of a lateral and main canal with supra- and sub-orbital branches.

(*b*) The presence of a series of small bony elements—drain-pipe-like canal bones—conducting either the canals or their branches.

(*c*) The presence of primitive pores upon the head.

(*d*) The absence of either a pre-orbital or an ethmoidal commissure.

xiii. Comparison of the Selachoid Ganoids with the Elasmobranchii.

A comparison of the sensory canal system of the Selachoid Ganoids with that of the Elasmobranchii shows that there are many important features common to the two.

The distribution and number of the canals and branches in all the Selachoid Ganoids are undoubtedly of an Elasmobranch character. Firstly, there is the branching of the

lateral canal in Polyodon and Psepherus, developed to a greater extent in such forms as Tænura lymna, Dasybatus dipterurus, Alopias vulpes, Rhinobates planiceps, &c.[1]

The persistence of dermal canals in Polyodon and Psepherus, and the very slight development in these two forms, and complete absence in Acipenser, of any true mandibular or maxillary branches, are prominent characteristics of the Selachians and Batoidea. In the distribution and form of the sensory organs (cluster pores, &c.) there are many points of agreement.

The total absence or only slight development in the Elasmobranchs of commissures agrees with the condition found in Polyodon and Psepherus, whilst in Acipenser the presence of only one—the occipital—and the arrangement of the canals and branches in the commissural regions of all three genera, exhibits many close affinities to such forms as Heptabranchias maculatus, &c.

The number, form, and distribution of the cranial nerves of Polyodon resemble, in the branching of the buccalis division of the facial nerve, and in the distribution of the otic, &c., the condition described and figured by Ewart (**25** and **26**) in the Elasmobranchii.

Indeed, after the many anatomical relations that Polyodon exhibits with the Elasmobranchii—described by Bridge some years ago (**16**)—I should have been greatly surprised had there not been a similar agreement in the sensory canal system.

xiv. Comparison and Review of the System in the Ganoidei.

In comparing the sensory canal system in the existing Ganoids, it must be borne in mind that they are an order of fishes the families of which are widely separated from one

[1] The sensory canal system of all these forms has been carefully figured by Mr. S. Garman (**32**).

another, the intervening gaps being but very imperfectly bridged over by a series of still less perfect extinct forms whose fossil remains show, in most cases, few if any indications of the course of this system of canals (20).

Of the eight known genera of recent Ganoids I have examined specimens of all excepting Scaphirhynchus, which in all probability is very similar to Acipenser.

The Polyodontidæ are undoubtedly the most generalised family, and most closely related to the Elasmobranchii.

In the Acipenseriidæ we have a great advance upon anything seen in either of the genera in the preceding family, and yet the absence of mandibular and maxillary branches and the persistence of large numbers of primitive pores are features which are truly Selachian. Acipenser is the first species in the class Pisces in which the canal or its branches enters into the cranial elements.

Of the Teleosteoid Ganoids we have three families widely separated from one another.

The most interesting feature in the Lepidosteidæ is undoubtedly the greatly developed system of dendritic branches passing off from the main canal and entering into the various cranial elements. These fine branches anastomose and form a dense network. In this feature the system resembles in many ways that present in the Selachians. There are no branches on the lateral canal. In the pre-orbital region there are a number of fine branches which anastomose and form a commissure connecting the two supra-orbital branches, a condition peculiar to Lepidosteus osseus, so far as is at present known (19).

The Polypteridæ show a number of features not previously met with. In Polypterus (18) we note the absence of dendriform branching and primitive pores, and the small number of pores generally, the presence of a branch from the operculo-mandibular branch, which passes across the cheek-plate, and a fine canal passing through the series of canal bones (= intercalary ossicles of Traquair) which connects the main canal of the head with the operculo-mandibular branch. There are also

traces of a rudimentary or degenerate canal in the pre-operculum.

The system in Calamoichthys is practically the same as that described in Polypterus.

The family AMIIDÆ has been the most thoroughly studied of any of the Teleosteoid Ganoids (1). The branching of the lateral canal still persists in the posterior border of the scale, the canals of the head are almost wholly contained in the bones, dermal portions being exceedingly small. The cluster and primitive pores are much more specialised in character and fewer in number. There is little or no branching of the system upon the head, excepting in the pre-operculum, an operculo-mandibular branch being present. There is no connection between the two mandibular portions in the median symphysis of the lower jaw. Both occipital and ethmoidal commissures are present, and a similar form of branching in the pre-orbital region as was noticed in Polyodon.

Not a few writers have examined the sensory canal system with a view to ascertaining its value in classification. I am not aware that it has been used for such purposes, and from the variability of its nature I should much doubt its value if applied in any than a very general manner.

XV. CLASSIFICATION.

GANOIDEI.

Group 1. SELACHOIDEI, Bridge.

Sub-order 1. CHONDROSTEI, Müller.

Fam. i. POLYODONTIDÆ.

Polyodon, Lacép.
— folium, L., p. 507.
Psepherus.
— gladius, Martens, p. 519.

Fam. ii. ACIPENSERIDÆ.

Acipenser, Artedi.
— sturio, L., p. 521.
Scaphirhynchus, Heckel, p. 528.
— catephractus, Gray.

Group 2. TELEOSTEOIDEI, Bridge.

Sub-order 2. HOLOSTEI, Müller.

Fam. i. LEPIDOSTEIDÆ.

Lepidosteus, Lacép.
— osseus, L., p. 528.
— platystomus (Raf.).

Fam. ii. POLYPTERIDÆ.

Polypterus, Geoff.
— bichir, G., p. 528.
Calamoichthys, J. A. Smith.
— calabaricus, J. A. S., p. 529.

Fam. iii. AMIIDÆ.

Amia, L.
— calva, L., p. 529.

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DESCRIPTION OF PLATES 39 and 40,

Illustrating Mr. Walter Edward Collinge's paper, "The Sensory Canal System of Fishes."

FIG. 1.—Dorsal view of the skull of Polyodon folium, showing the cranial elements and canal bones. The stellate-shaped bones on the rostrum are shown on the left-hand side, and the epidermis also in the most anterior portion. Lettering as below.

FIG. 2.—Lateral view of Polyodon, showing the course and branching of the lateral canal, its position on the caudal fin, and the groups of primitive pores on the head, &c. Lettering as below. $\times \frac{4}{5}$.

FIG. 3.—Diagrammatic view of the side of the head of Polyodon, showing the course of the main canal of the head and its branches.

Lettering.—com. Commissure in occipital region. *c. p.* Cluster pores. *d. ec. eth.* Dermo-ect-ethmoid. *d. eth.* Dermo-ethmoid. *d. sph.* Dermo-sphenotic. *fr.* Frontal. *hyom. b.* Hyomandibular branch of the main sensory canal. *l. c.* Lateral canal. *l. c. b.* Branches of the lateral canal. *m.* Mouth. *M. C.* Main canal of the head. *Mn. b.* Mandibular branch of the main canal. *Mx. b.* Maxillary branch of the main canal. *nar.* Nares. *op.* Operculum. *or.* Orbit. *pa.* Parietal. *pp.* Primitive pores. *pt.* Post-temporal. *sp.* Spiracle. *S. or.* Suborbital branch of the main canal. *Sp. o.* Supra-orbital branch of the main canal. *x.* Branches in the pre-orbital region.

FIG. 4.—Longitudinal section through a cluster pore from the occipital region of the head of Polyodon. Lettering as below.

Fig. 5.—Longitudinal section through a primitive pore from the opercular region of the head of Polyodon.

Lettering.—*ep.* Epithelial cells. *n.f.* Nerve-fibres. *p.* Pit. *sen. o.* Sense-organs.

Fig. 6.—Sensory organs from the lateral canal of Polyodon.

Lettering.—*a.* Modified cluster pore. *b.* Sensory organ, unknown. *c.* Sensory organ, unknown, in group. *d.* Cluster pore undergoing division.

Fig. 7.—Canal bones.

Lettering.—*a.* Lateral view of the tooth-shaped bone in the anterior part of the rostrum of Acipenser, connecting the supra- and sub-orbital branches. × 3. *b.* The same, inner view. The apertures, *a′*, represent the passage of various branches, the ↑ indicates the course of the main branch. × 3. *c.* Disc-like bone from the lateral canal of Acipenser. × 5. *c′.* Disc-like bone from the lateral canal of Acipenser; natural size. *d.* Canal bones from the head of Polyodon. × 2. *e.* Canal bones from the sub-orbital branch of Acipenser. × 2.

Fig. 8.—Lateral view of the cranium of Polyodon, showing the exit of the cranial nerves. The opisthotic and pterotic are added from Bridge (**16**, pl. 55, fig. 3).

Lettering.—*a. n.* Anterior nares. *d. sph.* Dermo-sphenotic. *hy. g.* Articular groove for the head of the hyomandibular. *op.* Opisthotic. *ptr.* Pterotic. The foramina for the exit of the cranial nerves are indicated by their respective numbers I to X.

Fig. 9.—Copy of van Wijhe's figure (**82**, pl. xv, fig. 4) of Polyodon, showing the relations of the cranial nerves to the hyomandibular, &c. Lettering as below.

Fig. 10.—Corrected figure showing, in my opinion, the right position of the hyomandibular bone and cranial nerves, &c.

Lettering.—*c. h.* Cerato-hyal. *e. h.* Inter-hyal. *h. h.* Hypo-hyal. *h. m.* Hyomandibular. *l.* Mandibulo-hyoidean ligament. *l′.* Quadrato-suspensorium ligament. *le. p.* Ethmo-palatine ligament. *M.* Meckel's cartilage. *m. ad.* Mandibular adductor muscle. *pm.* Outgrowth of masseter muscle. *p. q.* Palato-quadrate. *q.* Quadrate. *r. m.* Ramus mandibularis, fascialis. *r. m′.* Ramus mandibularis, fascialis internus. *r. m″.* Ramus mandibularis, fascialis externus. *r. m. i.* Ramus maxillaris inferior, trigemini. *r. m. s.* Ramus buccalis. *r. o. p.* Ramus opthalmicus profundus. *r. o. s.* Ramus opthalmicus superficialis. *r. ot.* Ramus oticus. *sy.* Symplectic.

Figs. 11 and 12.—Diagrams illustrating the sensory canals of the head and part of the lateral canal of the trunk, and the nerves which innervate their sense-organs. The canals and branches are coloured yellow, the trigeminal nerve blue, and the facial red. The cranial nerves are numbered respectively I to X. On the left-hand side the connection between the supra- and sub-

orbital branches is not shown, in order to show the branching of the olfactory nerve. *L. C.* The most anterior portion of the lateral canal, where it joins with the main canal of the head, *M. C.*; in its course forwards it gives off the branches *Oc. com.*, *Hyom.*, *S. or.*, and *Sp. O.* *Hyom.* The hyomandibular branch, innervated by the ramus opercularis superficialis No. 4, *r. o.* 4. It divides into two smaller branches, viz. a mandibular, *Mn.*, and a maxillary, *Mx.* *S. or.* The sub-orbital branch passing posterior to the orbit and meeting with the supra-orbital, *Sp. o.*, in the region marked *Sp.* o^3. In the region *Sp.* o^1. short branches are given off. *S. S.* O^1. The combined supra- and sub-orbital branches which give off in their anterior portion the branches *S. S.* O^2. and *S. S.* O^3.; *S. S.* O^4. indicates where the combined branches make an outward curve and join with their fellow of the opposite side.

Lettering.—Hyom. Hyo-mandibular branch. *l.* Lateral division of the vagus. *l'.* Branch of lateralis vagi. *L. C.* Lateral canal of the trunk. *M.* Mouth. *M. C.* Main canal of the head. *Mn.* Mandibular branch of the hyomandibular branch. *Mx.* Maxillary branch of the hyomandibular branch. *N.* Nares. *Oc. com.* Branches from the main canal in the occipital region. *Or.* Orbit. *r. b.* Ramus buccalis, with the branches *a*, *b*, *c*, *d*, and *e*. *r. m.* Ramus mandibularis, trigeminal. *r. m'.* Ramus mandibularis, facial. *r. mx.* Ramus maxillaris. *r. o.* Ramus opercularis superficialis, with the branches 1, 2, 3, and 4. *r. o. p.* Ramus opthalmicus profundus. *r. o. s.* Ramus opthalmicus superficialis. *r. ot.* Ramus oticus. *r. p.* Ramus palatinus. *S. or.* Sub-orbital branch of the main canal. *Sp.* Spiracle. *Sp. o.* Supra-orbital branch of the main canal. *S. S. O.* The combined supra- and sub-orbital branch. *Vg.* Vagus. *V. gl.* Ganglion of vagus.

FIG. 13.—Dorsal view of the head of Acipenser. The sensory canal system is marked in red. Lettering as below. $\times \frac{1}{3}$.

FIG. 14.—Lateral view of the same. $\times \frac{1}{2}$.

Lettering.—d. eth. Dermo-ethmoid. *d. ec. eth.* Dermo-ect-ethmoid. *d. oc.* Dermo-occipital. *ep.* Epiotic. *fr.* Frontal. *M. C.* Main canal of the head. *oc. com.* Occipital commissure. *op.* Operculum. *or.* Orbit. *pa.* Parietal *pt.* Post-temporal. *S. or.* Sub-orbital branch. *s. o.* Sub-orbital bones. *Sp. O.* Supra-orbital branch. *Sq.* Squamosal.

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